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ON THE EVOLUTION OF *PIERIS NAPI* L.

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INTRODUCTION

Among Fennoscandian butterflies *Pieris napi* L. is one of those showing the most striking geographic variation. This is observed especially in the number of generations during the summer, and in the wing color and melanistic markings on the upper side of the wings in the females.

In the southern part of the area (ssp. *napi* L.) the butterflies emerge in May. Some pupae of the second generation hibernate (univoltine development) but most specimens emerge in July (bivoltine development). The pupae of the third generation in Sweden never emerge during the same year but hibernate together with univoltine pupae of the second generation. So the first generation of the next year consists of specimens from two different generations of the previous year. It may be noted that in more southern areas *P. napi napi* forms three generations of flying butterflies per year (Müller and Kautz, 1938).

In the northern parts of Fennoscandia (ssp. *bicolorata* Pet.) the first generation flies in June and the second in August. Here the second generation is much rarer than the first (fig. 1), and in the mountains (ssp. *adalwinda* Fruhst.) it has been found only once.

Where the second generation flies as late as August, the third one in these northern areas has no or only a very small chance to reach the pupal stage before the early winter. The species can hibernate only in the pupal stage and so all or most larvae of the third generation of northern *P. n. bicolorata* perish.

It has been shown that the difference in number of generations between populations is in part inherited, in part directly induced by differences in the environment (Petersen, 1947, p. 418). When specimens from different parts of Sweden are reared at a constant temperature, the frequency of bivoltinism is highest in those from the south and decreases to the north. But the frequency of bivoltinism is also higher when specimens from the same locality are reared in a high constant temperature than in a low one. This agrees with Dawson's (1931) findings with the polyphemus moth.

The difference in number of generations in nature is of course partly a modification due to different climates in different parts of the area. But it is now possible to understand how an inherited geographic variation in voltinism can evolve. In the north, genes for bivoltinism must be unfavorable, as all or most descendants from the second generation (bivoltine specimens) do not survive.

In the south (range of *napi*), on the other hand, bivoltinism must be an ad-

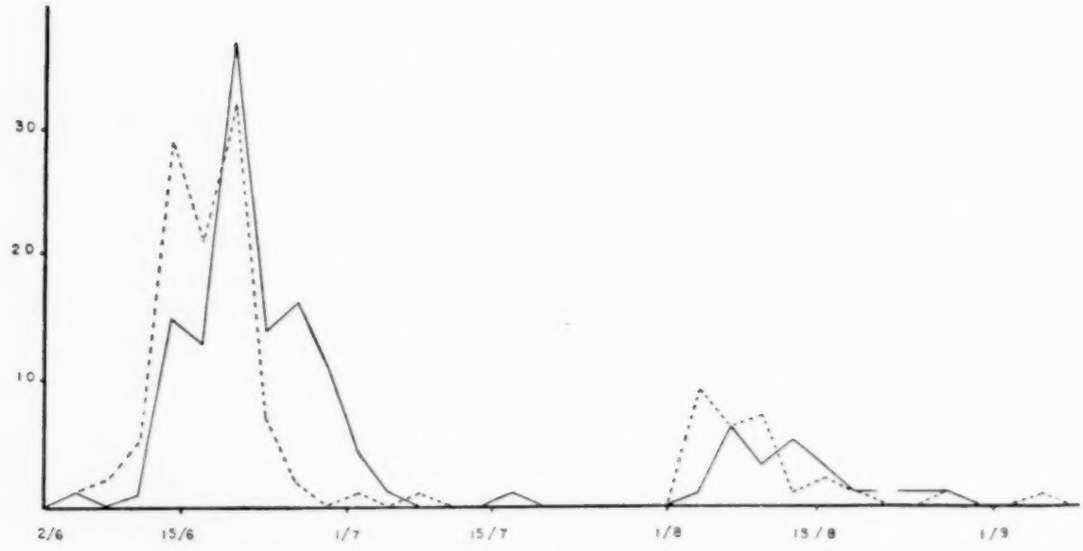

FIG. 1. Number of collected specimens of males (broken line) and of females (solid line) of *Pieris napi* in Pelkosenniemi (northern Finland, 67° latitude) during the summer 1947. On the abscissa the collections were combined in three-day intervals. The summer 1947 was extremely warm, so that the two generations must be assumed to come a little later in normal years.

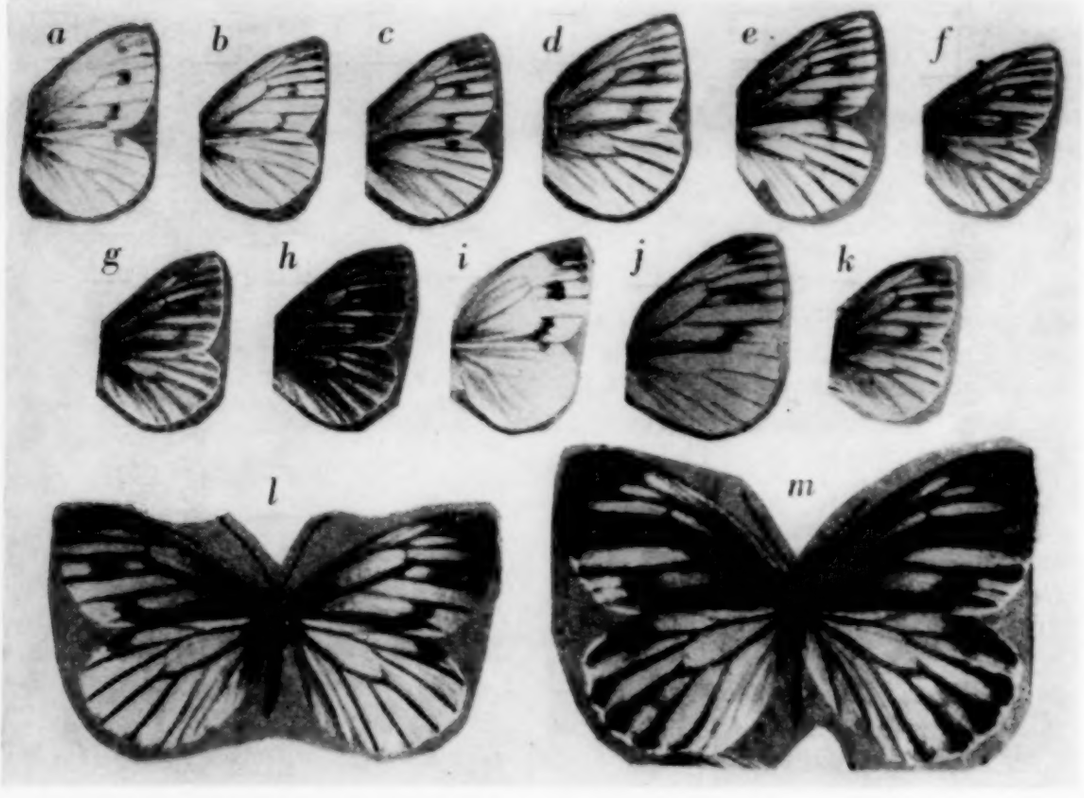

FIG. 2. a–c, melanistic markings of *P. napi napi* ♀, 1st generation; d–h, darker specimens occurring in *P. n. bicolorata* and *adalwinda* (the melanism of the apical spot is not included in the series); i, melanistic markings of *P. napi napi*, 2nd generation; j, k, darker specimens of the 2nd generation; l, *Pieris melete orientis;* m, *P. melete alpestris* (l and m after Verity, 1905–1911).

vantage, as bivoltine individuals may multiply during the latter part of the summer, while the univoltine ones rest in the pupal stage exposed to various dangers.

In *P. n. napi* ♀ the variation in color on the upper side of the wings is very slight, as almost all specimens are white. Of 380 Swedish specimens only one was classified as yellow, and the border line cases were almost negligible. In southern Finland yellow ones are more common. The frequency of white specimens decreases to the north and is lowest in the mountains.

The melanistic markings of *P. n. napi* are thin and well defined (cf. fig. 2 a–c, i). The darker forms occurring in the north have broader markings with dark scales among the white near the markings (fig. 2 d–h, j, k).

Geographic variation in both characters is genetically controlled (Petersen, 1947).

During further studies of the geographic variation of *P. napi,* I was struck by the fact that the northern forms of the females in Sweden begin to occur at the same latitude where the second generation begins to decrease in frequency. It seemed possible to me that there might be a correlation between the ways in which selection causes geographic variation of the three characters.

Material and Method

All specimens of *P. n. bicolorata* from localities where more than one specimen from each generation was available were examined. The investigation was made in the following way. Each specimen was classified for each character whether it ranged within the variation of *P. napi napi* or not.

As there is a non-genetic, seasonal dimorphism present, especially in wing markings, different scales were used for the first and the second generation. In this character, however, there is a rather marked "jump" between those ranging within and outside the variation of *P. n. napi,* so the source of error in using different scales for the two generations cannot be great.

For wing color we can, as an approximation, put *napi*-like = white. A very slight yellow also occurs in *P. n. napi* and was counted as white. The dividing color shade was a little more yellow in the first generation.

The melanistic markings of *napi*-like specimens are shown in figure 2 a–c, those of non-*napi*-like in 2 d–h. The difference in the second generation is exemplified in figure 2 i, j, and k. In addition to the differences already mentioned we may note that in *P. n. napi* dark scales cover only the outer parts of the veins on the upper side of the back wings just near the edge and they are sometimes lacking. In some specimens of *P. n. bicolorata,* on the other hand, the veins are covered with dark scales that extend into the cell (cf. fig. 2 k).

The results of the classification are shown in table 1. Only in one case (in wing color in the specimens from Haapavesi) are *napi*-like specimens significantly more frequent in the second generation than in the first ($\chi^2 = 4.01$ with Yates' correction). The significance of this is strengthened by the fact that two of the three other cases show a non-significant difference of the same kind.

As to melanistic markings, a significant level is not reached. In three cases, however, the *napi*-like specimens are more frequent in the second generation than in the first.

Discussion

A higher frequency of white wing color in the second generation than in the first can be explained in the following ways:

1. It is possible that some *bicolorata*-specimens have a genetical constitution which in the first generation gives yellow wings, in the second generation, white ones.

2. In the north, populations occur with hereditary univoltinism and yellow wing color; in the south, they are bivoltine and have white wings. If dispersal pressure

TABLE 1. *Number of specimens of* Pieris napi bicolorata ♀ *from four localities in Finland and Sweden, which resemble and do not resemble specimens of the same generation of* P. n. napi

Locality	Wing color				Melanistic markings			
	1st gen.		2nd gen.		1st gen.		2nd gen.	
	napi-like	non-*napi*-like	*napi*-like	non-*napi*-like	*napi*-like	non-*napi*-like	*napi*-like	non-*napi*-like
Finland								
Om Haapavesi, 1946	37	16	14	0	46	7	13	1
Lkem Pelkosenniemi, 1947	15	93	4	18	58	50	13	9
Sweden								
Jmt Ottsjön, 1944	46	14	1	2	44	16	2	1
Nb Piteå 1943, 1945	9	10	4	3	16	3	6	1

is high enough to bring mated females from rather different areas together, this might cause a correlation such as that which occurs. The marked geographic variation shows, however, that dispersal cannot be *very* high in the species, and therefore this explanation is very improbable, especially as dispersal of the earlier emerging males tends to diminish the correlation.

3. On the other hand, genes for the two characters can be closely linked, so they keep together for many generations without crossing over. In that case, a much lower dispersal pressure is needed.

If this explanation is correct, linkage will serve to separate two forms, one of which is better adapted in the north, the other in the south. It will tend to make the cline steeper, but it can not be an explanation of the evolution of geographic variation of wing color.

4–5. Two other possibilities can explain such an evolution. The first is that the combinations bivoltinism—white wing color and univoltinism—yellow wing color have a higher selective value than the other two combinations. The second is that genes, which influence wing color, also contribute to the determination of pupal development.

It is not possible to decide which of these explanations is correct, or if a combination of them is present. A discussion of the last possibility is, however, valuable from another point of view, and it will therefore be treated in a little more detail.

In many insects a correlation between some of the following characters has been found: Dark pigmentation, a slow rate of development, univoltinism, sluggish behavior, and a cold and damp climate (Kühn and Henke, 1929, 1932; Dawson, 1931; Kühn and von Engelhardt, 1937; Hovanitz, 1947, 1948).

These correlations are in no way surprising, if we consider the occurrence of homologous hormonal systems acting in a similar way during embryonal development in such different animals as *Drosophila, Ephestia,* and *Habrobracon* (cf., e.g., Becker, 1938). It is therefore easily understood that a mutation which changes the hormonal secretion may have a similar pleiotropic effect in different groups of animals.

P. napi shows clearly that sweeping generalizations are dangerous in cases like these. Here the dark pigmentation of most pattern elements is strongest in *P. n. adalwinda.* The apical spot and the wing spot, however, are smaller in this subspecies than in the others.

In these respects our knowledge of *P. napi* is rather scanty, if we exclude correlation between pigmentation and climate, as no experiments have yet been made. The flying time of the different forms can, however, give some information. The mean day was therefore calcu-

TABLE 2. *Mean date (in June) on which different forms of* P. napi bicolorata *(1st generation) were collected at two Finnish localities*

Locality	Wing color		Melanistic markings	
	napi-like	non-*napi*-like	*napi*-like	non-*napi*-like
Pelkosenniemi	21.5	21.5	20.3	22.8
Haapavesi	18.8	18.1	19.0	18.7

lated on which the different forms of the first generation in Pelkosenniemi and Haapavesi were caught. They are tabulated in table 2. Haapavesi gives very little information, as the non-*napi*-like specimens here are very few (cf. table 1). An analysis of variance shows, on the other hand, that the darker specimens were caught later than the lighter ones in Pelkosenniemi ($v^2 = 4.55$; $0.05 > P > 0.02$). This indicates that the darker specimens either emerge later or live longer than the lighter, *napi*-like ones. It is not possible to decide which alternative is present, or if there may be a combination of them.

For our purpose this is, however, to a certain degree immaterial. The descendants of the darker, non-*napi*-like specimens will grow in a temperature which is on an average lower than that of the *napi*-like specimens due to the difference in flying time between the two (cf. fig. 1). The temperature in these northern areas, especially during the night, is much lower in the latter part of July, when it is getting dark, than earlier in the season.

A low temperature increases the frequency of univoltine specimens (Petersen, 1947). Thus the fact that dark specimens of the first generation fly later than light ones will tend to make the frequency of light, *napi*-like specimens higher in the second generation than in the first. This is also found in three of four populations investigated, but it is in no case established (table 1). In this way the dark form will be favored in the same area as univoltinism.

In *P. n. bicolorata* univoltinism is favored north of a certain limit, where it is not possible for the third generation to reach the pupal stage before winter. In the same subspecies the ratio of yellow and dark specimens, together with univoltinism, increases to the north. Though it has not been proved that selection acts in one of the ways mentioned here to cause geographic variation of wing color and wing markings, such a process seems rather probable.

It can, however, be easily shown, that the problem is not so simple as hitherto supposed. *P. n. adelwinda* (mountains) has a fast rate of development combined with univoltinism, yellow and dark wings. This conflicts with the correlation between slow rate of development and dark wings mentioned above. It is possible that univoltinism favors the evolution of dark wings, but other explanations are also conceivable. It is, however, evident that many factors influence the evolution of every character of a species.

Another factor which might play a certain rôle is that dark specimens are better adapted to absorb sunlight. This would favor them in the north and especially in the mountains, where summer is coldest. But the fact that many species are darkest in the northeastern woodland and lighter in the northwestern mountains shows that this factor is not decisive in many cases.

During the last 15 years summers in Scandinavia have been warmer than before. During this time the second generation of *P. n. bicolorata* has become much more common. This is surely a modification due to warmer temperature. At the same time the limit to the south of which bivoltinism is favorable must have been dislocated to the north. If the reasoning of this paper is right, this must cause a displacement of all isophenes treated here to the north. A study of this problem will perhaps give us a better view of the evolution in *P. napi* than we now have.

Geographic Variation

A comparison of the geographic variation in the characters wing color and wing markings shows that to some extent they depend on different factors. As the first generation is different from the second, only the first was used. The percentage of *napi*-like specimens in different Fennoscandian localities was mapped for both characters. The results are shown on figures 3 and 4.

The isophenes for 5% on the two maps agree very well. So do the isophenes for 95% in Sweden. In Finland and the adjacent parts of Sweden, however, the isophenes for wing color are more southerly than the corresponding ones for melanistic markings, whereas the opposite is the case in Sweden near the border of Norway. This difference is well established as it is supported in the former area in 17 out of 18 localities and in the latter in 5 without exception.

Figure 5 shows the two different types of clines along the lines A_1–A_2 near the Norwegian border and B_1–B_2 near the

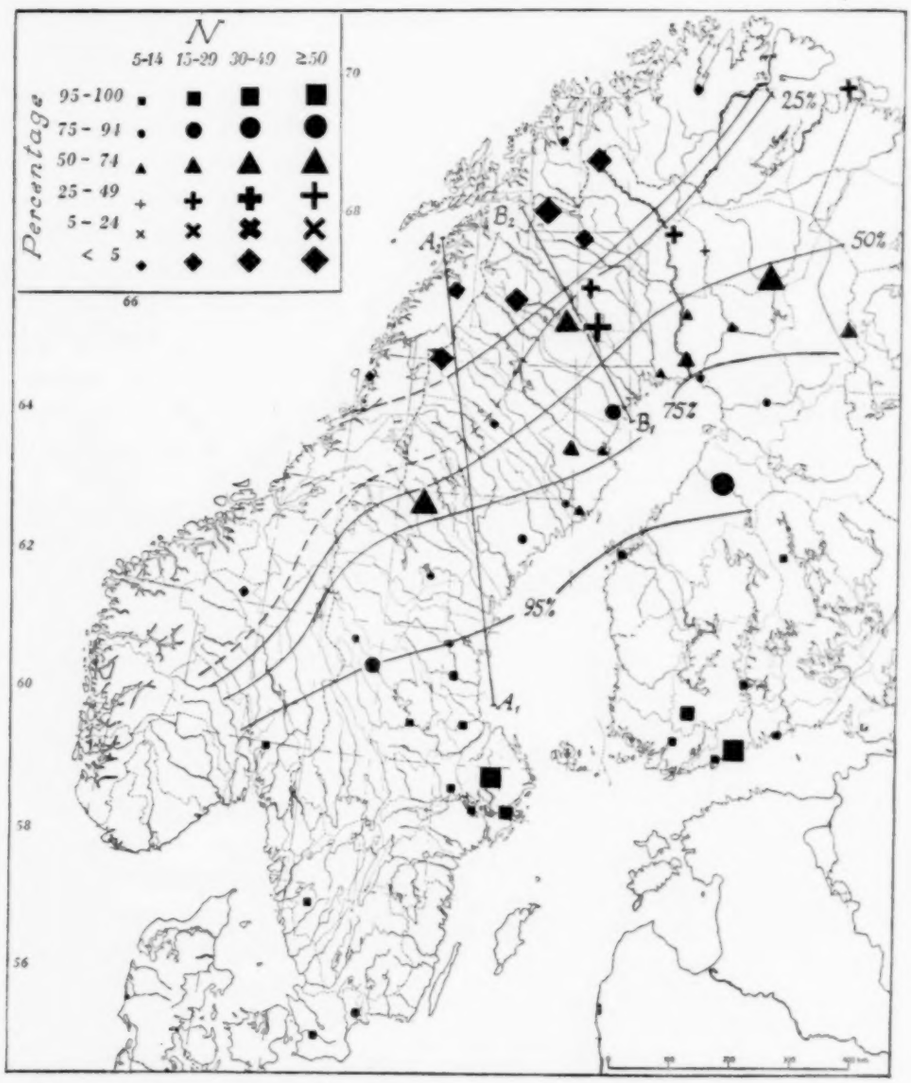

Fig. 3. Percentage at different Fennoscandian localities of specimens of *Pieris napi* ♀, 1st generation, the melanistic markings of which range within the variation of *P. napi napi* (cf. fig. 2, a–c). The northern limit of this subspecies may be put at the isophene 95 per cent, that of *P. n. bicolarata* at the isophene 5 per cent. The lines A_1–A_2 and B_1–B_2 are explained in the caption of figure 5.

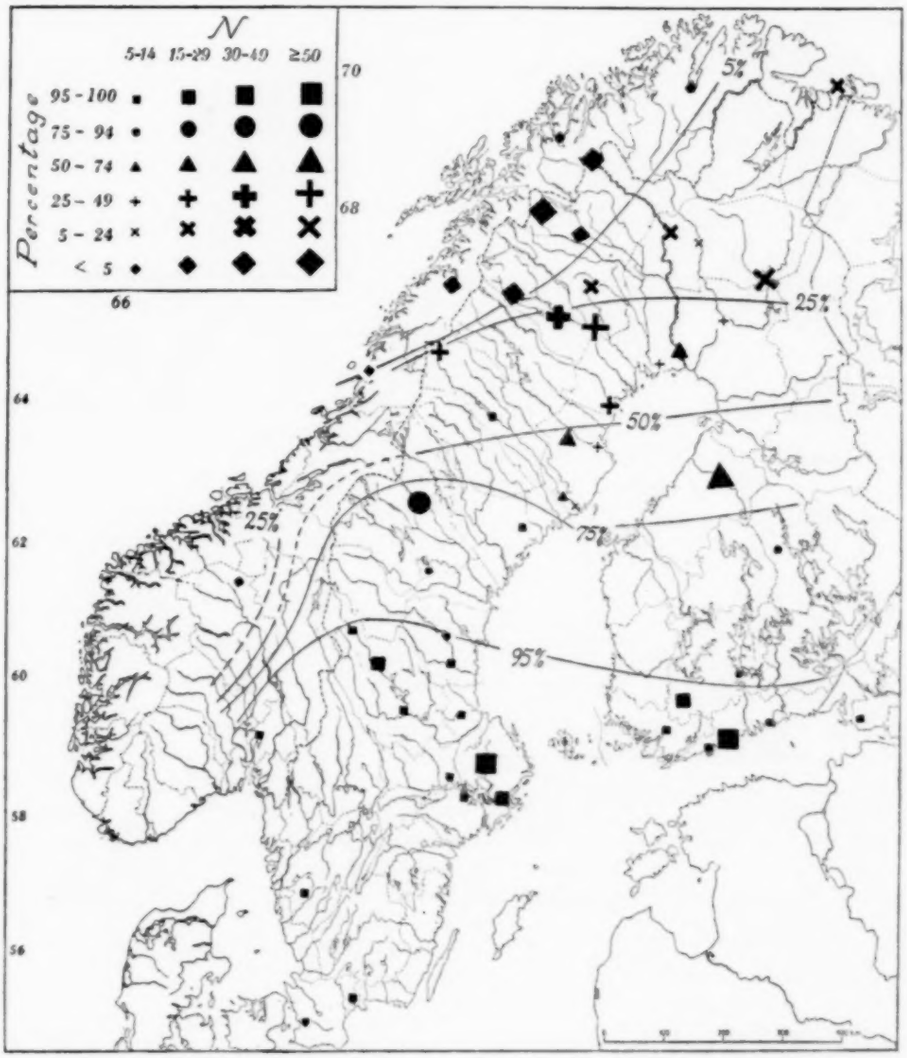

FIG. 4. Percentage at different Fennoscandian localities of white (*napi*-like) specimens of *Pieris napi* ♀, 1st generation.

Finnish border. The lines are shown on figure 3. In type A the cline for wing color lies above the cline for melanistic markings, in type B they have the opposite position.

It is impossible to decide which factor causes this difference in geographic variation of the two characters. It may, however, be pointed out that the area of cline type A, where the dark forms are more favored than the yellow, has a wetter and damper climate than that of cline type B.

In its extra-Fennoscandian distribution area, *P. napi* is in many localities represented by subspecies with yellow and dark females as in the Fennoscandian mountains. They have been found in the Alps, Carpathians, Caucasus, Naryn (Turkestan), Tian Shan, Sajan, Altai, Vitim, Kamchatka, Alaska, Labrador and on Caribou Island. In a less pronounced form they occur even in other localities, e.g., in Great Britain (Verity, 1905–11; Röber, 1908; Müller and Kautz, 1938).

Almost all of these localities are northern or situated in mountains. The number of generations is in most cases unknown, and for our purpose it is necessary to ascertain whether or not the descendants from the second generation are able to pupate before winter. We know that in the Alps and Carpathians the spe-

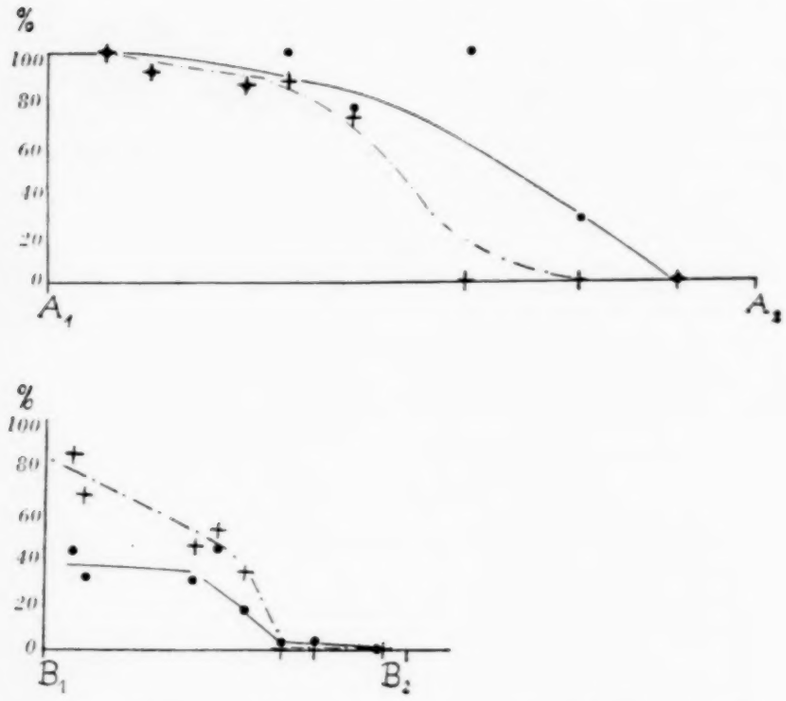

FIG. 5. Percentage of *napi*-like specimens along the cross sections A_1–A_2 and B_1–B_2 through Scandinavia (see map, fig. 3). Wing color (solid line and dots) and melanistic markings (broken line and crosses). The distance of points in the graph between A_1 and A_2 and between B_1 and B_2 corresponds to the distances on the cross section (fig. 3). Localities are projected to the nearest point on the cross section. Only localities in the neighborhood of these cross sections have been included. The clines have been drawn weighted, i.e., consideration has been given to the number of specimens examined from each locality.

cies in the higher parts has only one generation (Müller and Kautz, 1938; Niesiolowski, 1936), and it is indicated in other cases.

Univoltinism seems therefore to occur in *P. napi* in those subspecies in which the females are yellow and dark. It seems very probable that in the different cases rather similar factors are at work to maintain those predominantly alpine races distinct from the surrounding forms of *P. napi*.

DIFFERENCE IN SPECIES

It has been supposed by many authors, especially by Müller (cf. Müller and Kautz, 1938), that *Pieris napi napi* and *P. napi bryoniae* of the Alps might be two different species. One of the chief arguments for this view is that *bryoniae* is usually singlebrooded, while *napi* has at least two generations. As has just been shown, a high frequency of *napi*-like specimens in the second generation accords with the opinion that the two forms belong to the same species.

I will further cite Müller and Kautz (1938, p. 58): "Wenn aus einem und demselben Gelege, wie dies bei *radiata* und *flavescens* [intermediate forms] die Regel bildet, Stücke mit der Bestäubung von *concolor* [the darkest *bryoniae*-form] in allen Übergängen bis zur schwächsten *napi*-Zeichnung schlüpfen. . . ." Since females of a certain phenotype never give offspring belonging to two different species, since both types and intermediates occur in the same localities and habitats, and since they are easily crossed in experiments, there is no reason to think

that we deal here with more than one species. Mayr (1942) also doubts the difference in species between *napi* and *bryoniae* on the basis of the facts mentioned by Müller and Kautz.

History

The evolution of *P. napi* can probably be explained in one of two ways. There may have existed an early form more or less similar to *P. n. bryoniae* which was able to survive in areas where the summer is cold and short. In this case the *napi* forms, when they evolved, replaced the others in areas with warmer climates or made it possible for the species to invade such areas.

If, on the other hand, the *napi* forms are older, it is possible that the *bryoniae* forms evolved independently in two or more places. This is a consequence of looking upon them as adaptations to an arctic-alpine environment.

Analogous conditions are of course present in the first case. But here it does not mean so much as the distribution area of the *napi* forms is more continuous.

This history of evolution must of course be regarded as schematic. It is very probable that the two types evolved so early that the species does not yet merit the name *P. napi*. Even in *Pieris melete* Mén., which replaces *P. napi* in the Himalayas and East Asia, females exist in some localities with white wing color and thin markings on the upper side, and in others with yellow wing color and strong melanistic markings (cf. fig. 2). These latter forms, more or less pronounced, occur in the mountains (ssp. *ajaka* Moore, *alpestris* Verity) (Verity, 1905–11, pp. 138–40). Thus it is impossible to decide which way the evolution of *P. napi* actually occurred.

Acknowledgment

The author wishes to express his appreciation to Mr. E. A. Hellman, Helsingfors, for collecting all specimens studied from Haapavesi and Pelkosenniemi.

Summary

In the northern parts of Fennoscandia univoltinism is favored in *P. napi* as descendants from those butterflies, that emerge late in the season, are exterminated. They can not reach the pupal stage on account of the cold and short summer. In southern areas they can pupate, and here bivoltinism is favorable, as only bivoltine specimens can multiply during the latter part of the summer.

In a population of *P. napi bicolorata* (northeastern Fennoscandia) univoltinism is correlated with yellow wing color and broad melanistic markings on the upper side of the female wings, bivoltinism with white color and thin markings. The same correlation occurs also in the geographic variation of the species. A selective advantage of the bivoltine and the univoltine types in different areas will probably also influence the geographic variation of wing phenotypes and so contribute to cause or at least maintain the variation.

As the geographic variation of the two wing characters is different (figs. 3–5), it is not possible to explain them as caused by a single selective factor.

No valid reasons have been advanced by other authors for the view that *P. napi napi* and *P. napi bryoniae* of the Alps should belong to two different species. On the contrary, all facts speak in favor of their being geographic races of the same species.

The first differentiation in *napi*-like (bivoltine) and *bryoniae*-like (univoltine) forms must have occurred very early, as the same differentiation is also present in the closely related *P. melete*. Different ways in which the species may have evolved are discussed.

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SOME PROBLEMS IN THE EVOLUTION OF A GROUP OF ECTOPARASITES

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The Mallophaga are a group of ectoparasitic insects found on birds and mammals. Their complete life-cycle from egg to egg is spent on the same host form, away from which, under natural conditions, they cannot feed nor live for more than a short time. This group is of especial interest in that a large number of species may be found on one host. Most bird groups have five or six species of Mallophaga and some many more. Twelve species of Mallophaga belonging to eight genera and three families have been recorded from one species of Tinamidae (Tinamous), *Crypturellus obsoletus punensis,* and fifteen species belonging to twelve genera and three families from another, *Tinamus major.* In this paper the various factors which may have been responsible for speciation in this group of parasites are discussed and comparison made with the process of speciation in free-living animals.

I. THE PRESENT DISTRIBUTION AND HOST RELATIONSHIPS OF THE MALLOPHAGA

The Mallophaga or chewing lice are placed as one of the sub-orders of the Phthiraptera, the other being the Anoplura or sucking lice of mammals. It is commonly assumed that the order is derived from a primitive Psocid-like ancestor which became parasitic first on birds. Both Harrison (1914, 3) and Webb (1946, 100) agree that the Mallophaga of mammals were derived from bird Mallophaga after these were already specialized for the parasitic habit; Webb (*loc. cit.*) suggests that migration from bird to mammal took place more than once. Hopkins (in press) considers this assumed avian origin of the Mallophaga not improbable but unproved and by no means certain. Webb also suggests (1946, 101) that the Anoplura or sucking lice, found only on mammals, were derived from one of the Ischnocera (the more specialized superfamily of the Mallophaga further discussed below); this ancestral Ischnoceran is presumed to have migrated from bird to mammal where it gave rise to two branches, the descendants of one being the Anoplura, and of the other the Ischnoceran Mallophaga found on mammals. This implies that the Ischnocera (Mallophaga) on mammals are more closely related to the Anoplura than to the other superfamily of Mallophaga (the Amblycera) found on mammals and to all the Mallophaga of birds, and, of course, makes the present division of the order into two suborders—the Mallophaga or chewing lice and the Anoplura or sucking lice—phylogenetically incorrect.

The Mallophaga are separable into two, extremely distinct, superfamilies—the Amblycera and Ischnocera. The Amblycera (fig. 1a) have retained more of the habits and morphological characters of the ancestral free-living insect than have the Ischnocera (fig. 1b–f), and, in general, are probably not so restricted to definite habitats on the body of the host. This lesser degree of specialization for particular habitats has resulted in fewer and less extreme ecological types on any one host species—of the fifteen species found on *Tinamus major,* only one is a member of the Amblycera. This is reflected in the classification, the Amblycera being contained in about fifty homogeneous genera, while the Ischnocera are divided into nearly a hundred genera (the conception of large genera being adopted here),

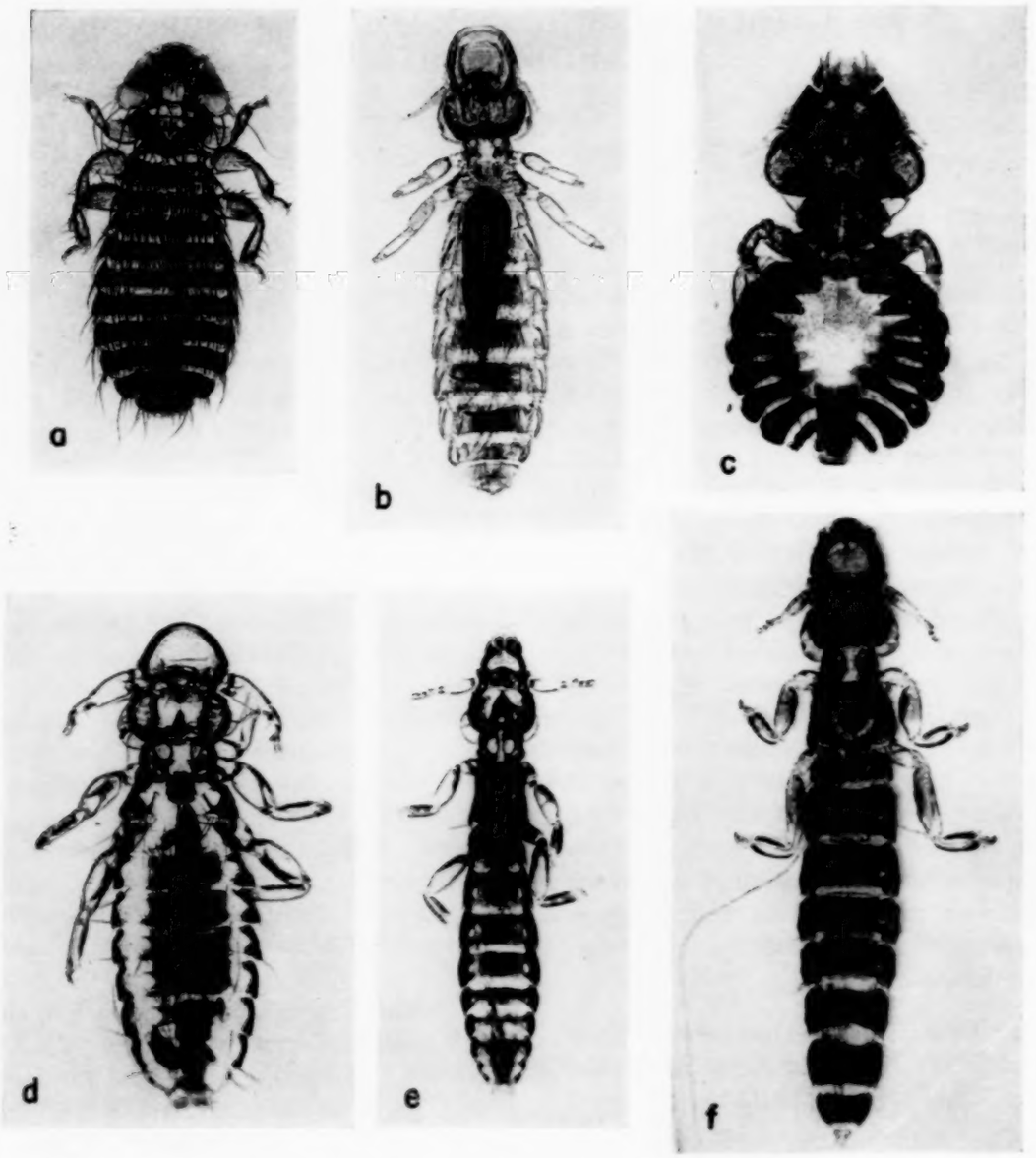

FIG. 1. a. Species of the superfamily Amblycera from the Anseriformes. b–f. Species of the Superfamily Ischnocera. b. *Degeeriella* species from the Falconiformes. c. *Craspedorhynchus* species from the Falconiformes. d. *Cuclotogaster* species from the Galliformes. e. *Fulicoffula* species from the Rallidae. f. *Perineus* species from the Procellariiformes.

many of which are divisible into well-marked species-groups. Hence, the problem of the multiplicity of forms in the Mallophaga is better illustrated by the Ischnocera, and examples from this superfamily will mostly be used, and as the groups living on avian hosts are better known to the present writer than those on mammalian, no examples will be taken from the latter.

The Ischnoceran population of any one host species belonging to the majority of avian orders is separable into a number of morphological types which occupy the different ecological niches found on the body of the bird. On the head and neck of the bird, for instance, is found a short, round-bodied type, not greatly flattened dorso-ventrally, and with a large head to accommodate the enlarged mandibles and

their strong supporting framework (fig. 1c). This type is adapted to movement on the shorter, narrower feathers of the head and neck, and, because its habitat is out of reach of the bird's bill during preening, it could develop the larger mandibles which meant an increase in head size; this type found on any other part of the bird would be easily picked off or crushed by the bill during the preening of the plumage. On the longer, broader feathers of the back and wings there is found a flattened elongate type (fig. 1e–f) which can slip sideways across the breadth of the feathers with great rapidity. The enlarged mandibles with the correlated increase of head size are not found in any of the typical wing-lice. Examinations of freshly killed birds show that these habitat forms are not found outside their own territories, except sometimes in the case of abnormally heavy infestations; the eggs of the head louse are laid on the feathers of the head and neck and those of the wing-louse on the wings and their axillary feathers. Apart from these two ecological types there are others, differing in size and body form, which either inhabit different parts of the plumage or are of the more primitive type (fig. 1b) and may not be so closely restricted and specialized for any one habitat; unfortunately there is little information available on the normal location of many of the species of Mallophaga.

That there is a general correlation between size and shape of the Mallophaga and size of feathers is suggested by the absence of the typical wing lice genera (that is with the elongated body and ventral genital opening in the male, fig. 1e–f) on those orders containing the smaller birds, for example, the Passeriformes (Perching birds); or on the smaller members of an order. Thus the wing louse genus *Falcolipeurus* of the Falconiformes (Birds of Prey) is not found on the smaller hawks. Where the typical wing louse is absent its place is taken by a narrow form with shortened abdomen and with the male genital opening in the dorsal position (fig. 1b) as in *Bruelia* of the Passeriformes and *Degeeriella* of the Falconiformes. On any one host species there may be two or more related genera derived from each ecological type, and each of these sympatric genera may have two or more sympatric species.

The development of feathers by the ancestral birds or hair by the ancestral mammals provided a new type of habitat —an empty ecological niche—and it might be expected on the analogy of other groups, that the colonization of a new habitat, where food was plentiful and competition lacking, would result in the rapid evolution of the ancestral Mallophaga; the different ecological niches on the host's body, as these were formed during the evolution of the birds, would be occupied, with the ensuing adaptations of the louse. Superimposed on this process, which might be called evolution in space, was evolution in time caused by each habitat type having to adapt itself to the changes of its own particular ecological niche, these changes being brought

TABLE 1. *Examples of host groups with specific genera of typical head and wing lice*

Position on the bird of starred genera not recorded.

Host group	Genus of head louse	Genus of wing louse
Tinamiformes (Tinamous)	**Pseudophilopterus*	*Pseudolipeurus*
Procellariiformes (Petrels)	*Trabeculus*	*Naubates*
Pelecaniformes (Pelicans, cormorants and allies)	—	*Pectinopygus*
Ciconiiformes (Herons and storks)	*Ibidoecus*	*Ardeicola*
Anseriformes (Ducks, geese, and swans)	*Anatoecus*	*Anaticola*
Falconiformes (Birds of prey)	*Craspedorrhynchus*	*Falcolipeurus*
Rallidae (Rails)	*Incidifrons*	*Fulicoffula*
Momotidae (Motmots)	**Clayiella*	—
Meropidae (Bee-eaters)	*Meropoecus*	—
Rhamphastidae (Toucans)	**Austrophilopterus*	—
Passeriformes (Perching birds)	*Philopterus*	—

about by the evolution of the birds themselves. The environment of the Mallophaga is formed by the chemical composition and physical structure of the feathers, the texture of the skin and certain physiological characters of the host such as temperature and body secretions. Thus, each ecological type, as the result of changes in these characters of their hosts, evolved with their hosts, but, in general, at a slower rate (that is after the initial period of rapid evolution); this is reflected in the general correlation found between the classification of host and parasite. It is usual to find a genus of Mallophaga restricted to an order of birds (table 1) [there are, however, a considerable number of exceptions (tables 2 and 3), the reasons for which will be discussed below], and within the parasite genus each species will usually be restricted either to one host species or subspecies (tables 4 and 5 and see Eichler, 1946, 10–11 for other examples), or to a group of related host species (table 6).

TABLE 2. *Examples of genera or groups of closely related genera of Ischnocera with unspecialized heads, or Amblycera, found on more than one host group*

Names in brackets will, in many cases, probably prove to be congeneric with the preceding genus. Starred genera belong to the superfamily Amblycera

Genus or closely related group of genera of Mallophaga	Host group on which found
Otidoecus (*Otilipeurus*), *Rhynonirmus* and *Cuclotogaster*	Otides (Bustards) Charadriiformes (Shore-birds) Galliformes (Game birds) Musophagi (Plantain-eaters)
Goniodes, *Goniocotes*, *Coloceras*, and *Campanulotes*	Galliformes Columbae (Pigeons and Doves)
Lagopoecus and *Tinamotoecola*	Galliformes Tinamiformes (Tinamous)
Degeeriella (*Cuculicola*, *Trogonirmus*, *Capraiella*, *Upupicola* and *Picicola*)	Falconiformes (Birds of prey) Cuculi (Cuckoos) Trogoniformes (Trogons) Coraciidae (Rollers) Upupidae (Hoopoes) Pici (Woodpeckers) Passeriformes (Perching birds)
**Colpocephalum* (*sens.* Clay, 1947 (1))	Pelecaniformes (Pelicans, cormorant and allies) Ciconiiformes (Herons and storks) Anseriformes (Ducks, geese, and swans) Galliformes Cariamae (Cariamas) Columbae Strigiformes (Owls) Pici Passeriformes
**Menacanthus* (*sens.* Clay, 1947 (1))	Tinamiformes Galliformes Musophagi Upupidae Capitonidae (Barbets) Rhamphastidae (Toucans) Pici Passeriformes

TABLE 3. *Examples of genera or closely related groups of more specialized genera of Mallophaga found on more than one host group*

Explanations of these cases of anomalous distributions of Mallophaga genera given in the text. Names in brackets will, in many cases, probably prove to be congeneric with the preceding genus

Genus of closely related group of genera of Mallophaga	Host Group on which found
a. *Aptericola*, *Wilsoniella*, *Rallicola* (*Parricola*, *Furnaricola*)	Apterygiformes (Kiwis) Opisthocomi (Hoazin) Rallidae (Rails) Charadriiformes Cuculi Passeriformes
b. *Saemundssonia*	Procellariiformes Gruidae (Cranes) Charadriiformes
c. *Ibidoecus*	Ciconiiformes Aramidae (Limpkins)
d. *Oxylipeurus*, *Splendoroffula*	Galliformes Musophagi
e. *Anatoecus* (Ischnocera, head louse) f. *Anaticola* (Ischnocera, wing louse) g. *Trinoton* (Amblycera)	Anseriformes Phoenicopteridae (Flamingoes)

If it is assumed that the above outline gives a general picture of the course of evolution in the Mallophaga, can this be explained by the theory of speciation by geographical isolation as applied to free-living animals? The possible factors responsible for speciation and for the present distribution of the genera and species of the Mallophaga will be discussed below under three main headings: Isolating factors, Ecological factors, and the Origin of sympatric species. The word "speciation" is used for the process of bringing about any new form, whether the present product is now a species, genus or family.

II. Isolating Factors in Mallophaga Speciation

1. Isolation by species formation in the hosts

The host distribution of the Mallophaga is the equivalent of the geographi-

cal distribution of the free-living animal. If the populations of any host species are in continuous contact then potentially the parasite can move throughout the species, but if the host species is divided into isolated or semi-isolated populations it follows that the louse population will be likewise divided. If one of these isolated populations of the bird species gives rise to a new species and even if later becomes sympatric with its parent population there would be no further interchange of lice owing to the discontinuance of interbreeding between the two bird populations, now distinct species. Here, therefore, is

TABLE 4. *Examples of related host species or subspecies each with an allopatric species of a Mallophaga genus*

Some of the Mallophaga species will probably prove to be subspecies. Percentage of host species in the genus *Crypturellus* (*C.*) (Tinamiformes) from which *Strongylocotes* (*S.*) is known is 52.2%, *Austrokelloggia* (*A.*), 43.5% and *Pectenosoma* (*P.*), 47.8%

Host species from which Mallophaga known	Mallophaga species
Crypturellus cinereus	*Strongylocotes abdominalis* *Austrokelloggia heterurus*
C. o. obsoletus	*S. complanatus*
C. o. ochraceiventris	*S. intermedius*
C. o. punensis	*Pectenosoma punensis* *A. obsoletus*
C. soui nigriceps	*A. nigriceps* *P. nigriceps*
C. s. mustelinus	*S. perijae*
C. s. albigularis	*S. albigularis*
C. s. inconspicuus	*S. subconiceps* *A. inconspicuus* *P. inconspicuus*
C. s. meserythrus	*P. meserythra*
C. u. undulatus	*A. undulatus*
C. u. yapura	*P. yapurae*
C. b. boucardi	*S. boucardi* *A. boucardi* *P. boucardi*
C. garleppi affinis	*S. interruptus* *P. angusta*
C. v. variegatus	*A. coniceps* *P. verrucosa*
C. v. salvini	*S. variegatus*
C. c. cinnamomeus	*S. fimbriatus*
C. c. idoneus	*A. idoneus*
C. c. sallaei	*P. cinnamomea*
C. n. noctivagus	*S. noctivagi*
C. t. tataupa	*S. glabrous* *A. genitalis* *P. parva*
C. parvirostris	*A.* n. sp. *P.* n. sp.

TABLE 5. *Examples of host groups where ratio of known species of Mallophaga is to host species as 1:1*

Host group	Percentage of host species in the group from which Mallophaga species of the genus is known	Mallophaga genus
Charadriiformes (Shore birds)		
Chettusia	100%	*Quadraceps*
Hoplopterus	100%	*Quadraceps*
Charadrius	45%	*Quadraceps*
Tringa	77.8%	*Quadraceps*
Actitis	100%	*Quadraceps*
Heteroscelus	100%	*Quadraceps*
Pterocletes (Sand-grouse)		
Syrrhaptes	100%	*Syrrhaptoecus*
Pterocles	81.2%	*Syrrhaptoecus*
Anseriformes (Ducks, geese, and swans)		
Cygninae	71.4%	*Ornithobius*
Galliformes (Game birds)		
Alectoris	100%	*Cuclotogaster*

TABLE 6. *Examples of groups of related host species each with an allopatric species of a Mallophaga genus*

Hosts	Percentage of host species in group from which Mallophaga known	Mallophaga species
Galliformes, Tetraonidae (Grouse)		
Tetrao urogallus *T. parvirostris*	100%	*Goniodes bituberculatus*
Lyrurus tetrix *L. mlokosiewiczi*	100%	*G. tetraonis*
Dendragapus obscurus	100%	*G. simoni*
Lagopus scoticus *L. lagopus* *L. mulus* *L. leucurus*	100%	*G. lagopi*
Canachites canadensis	100%	*G. corpulentus*
Bonasia umbellus	100%	*G. bonasus*
Tympanuchus cupido	50%	*G. cupido*
Centrocercus urophasianus	100%	*G. centrocerci*
Pediocetes phasianellus	100%	*G. nebraskensis*
Charadriiformes, Sterninae (Terns)		
Chlidonias hybrida *C. leucoptera* *C. nigra*	100%	*Saemundssonia lobaticeps*
Sterna aurantia		*S. hopkinsi*
S. hirundo	22.6%	*S. sternae*
S. paradisaea		*S. lockleyi*
S. vittata		
S. albifrons		*S. melanocephalus*
Thalasseus bergii *T. bengalensis* *T. sandvicensis*	42.8%	*S. laticaudata*

the exact analogy of the situation found on a group of continental islands, the populations of which have become isolated by the disappearance of land connections. Within each ecological niche on the body of the bird, these isolated populations of lice would have become modified through adaptations to the changing environment brought about by the changes in the evolving bird, as does a free-living animal to the climatic and other changes acting in its ecological niche (further discussed below under section III).

2. Isolation by the development of host specificity

In the Mallophaga dispersal can take place during brooding of the young birds (the case of brood parasites will be discussed below), during copulation, and during roosting in gregarious birds; all these interchanges of lice are between individuals of the same host species. Movement of Mallophaga individuals from one host species to another must be rare, as normally birds of different species do not come into close enough contact for such transference. Interchange can, however, take place between predator and prey, nestling and foster parent in brood parasites, by the use of common dust baths (Hoyle, 1938) and by phoresy (discussed below). In addition to the difficulty of transport from one host to another, the migrant louse must be able to establish itself on the new host. This may be prevented not only by the competition of the already established and better adapted resident louse population, but the immigrant louse may be strongly host specific, so that it is unable to feed or its eggs and nymphs develop on any but its own host species (Wilson, 1934, 308). The transference either of individuals of both sexes or of a fertilized female must of course take place. That establishment is not only a question of transference and lack of competition is shown by the cases of brood parasites, where there is ample opportunity for transference during brooding of the young, and no competition from an established population on the new host. The European cuckoo (*Cuculus canorus*), a brood parasite, has species of three genera of lice found on the Cuculidae throughout the world which are distinct from those of the Passeres, the suborder to which the foster-parents belong; thus, in spite of optimum conditions for transference the lice of the latter have never been able to establish themselves on the cuckoo. It is not known to what degree host specificity is carried and it is possible that lice could and do establish themselves on related hosts, the rare occurrence of this being due more to the difficulties for the louse of passing from one host species to another than to its establishment on the new species. The many cases of established populations of *Lipeurus caponis*, a normal parasite of the chicken, on pheasants, partridges, and guinea fowl, the eggs of which have been hatched under chickens, show that it is possible (see Eichler, 1940, for other examples), and will be further discussed below. The normal isolation of the populations of Mallophaga of any one host species, due to the difficulties of a louse passing between hosts of different species, has allowed the close adaptation of the parasite to the environment provided by its particular host, and has thus led to the development of host specificity. This host specificity will increase the isolation of the louse populations by making it more unlikely that an immigrant louse will be able to establish itself on a new host and thus interbreed with the resident louse population. This isolation has led, as in the case of island populations, to the formation of species—each restricted to the island in the case of the free-living animal and to the host species in the case of the parasite.

3. Isolation and reunion of host populations

During the evolution of the birds there must have been frequent geographical isolation of parts of the population of a bird species which reunited before any repro-

ductive isolating mechanism had developed. The reunion of the bird populations would mean the merging again of their louse populations, but it is possible that during the period of isolation one of the louse populations might have developed some character which prevented free interbreeding with the parent population, thus forming two species. These species would gradually spread throughout the combined host populations until the host species was parasitized by two sympatric species.

4. Extinction of louse populations

The potential range of each species of Mallophaga is that of its host species, but collections of Mallophaga from one host species in different parts of its range show that there is a true geographical distribution superimposed on the host distribution. Such a geographical distribution may be found over quite small areas: for instance, in the British Isles populations of the chaffinch (*Fringilla coelebs*) or the robin (*Erithacus rubecula*) in one locality may be found with a high incidence of individuals infested with *Ricinus*, whereas in another locality infested individuals seem to be absent. Numerical data are scanty owing to the disinclination for the slaughter of large numbers of birds in one locality, but the following records suggest a geographical distribution for the parasite species concerned: *Laemobothrion* species from the coot (*Fulica atra*) never recorded from Great Britain (42 *), but known from Morocco (two infested individuals out of six examined) and India (two out of ten); *Laemobothrion* species from the moorhen (*Gallinula chloropus*) not recorded from Great Britain (75 *), but known from the Sudan (only one specimen examined); *Ricinus* species from the crested lark (*Galerida cristata*) not known from Egypt (one locality only, 13), nor Khartoum, Sudan (9), but found on five out of seven individuals from Atbara, Sudan; *Picicola* not known from the green woodpecker in the British Isles (11), but found in the only two individuals examined from Sweden; *Philopterus* species from the European robin known only from two records in the British Isles (147 * examined from Europe and N. Africa).

This type of discontinuous distribution of species may have had two important effects on speciation: (1) the isolation of populations by an intervening area of absence and (2) the emptying of a particular ecological niche enabling either another species on the same host or an immigrant louse from another host species to occupy it. If a host species, for instance, is spread across a continent and for some reason one of its louse species has become extinct in the middle of its range, then the two louse populations at either end of the range will be isolated. In time the louse species may again spread throughout the population of its host, but it is possible that in one of the populations some kind of sexual isolating mechanisms may have developed. Even where there is no temporary absence of a louse species the Mallophaga population of polytypic host species with a wide continuous range will tend to form distinct populations, potentially of subspecific value, as is found in free-living animals (Mayr, 1942, 180). Even the small amount of work done on this subject shows that this has happened: in the case of one of the louse species (*Cuclotogaster cinereus*) of the quail, specimens from the European quail (*Coturnix c. coturnix*) differ from those from the Far Eastern subspecies (*C. c. japonica*) in the proportions of the head, thorax, abdomen, and male genitalia (Clay, 1938, 149). No work has been done on the statistical examination of populations from different parts of the range of a polytypic species, which might show that such subspecies or microsubspecies are commoner than is now apparent.

Not only will some lice be absent in part of a bird's range but the population size of any given louse species may vary

* Numbers in author's own records only, the actual numbers examined would be greater.

enormously: for instance, a curlew (*Numenius a. arquata*) from Ireland had over 1,800 lice of three species; other specimens have been found with all but one of these species absent, and reduced to 10 or 20 in number. Examples of equivalent differences in population numbers of a single louse species could be quoted for almost any host species from which Mallophaga have been collected. This suggests that fluctuation in population sizes with the concomitant increased speed of genetic change may also play an important role in speciation in the Mallophaga.

There are two characters found in the Ischnoceran Mallophaga which, amongst others, may have been developed during these periods of isolation and have been responsible for sexual isolation between daughter and parent populations: these are (a) the proportions of the abdomen and (b) sexual dimorphism of the antennae.

(a). As already shown there is a tendency towards a shortening of the abdomen in certain of the ecological types; this shortening must affect the method of copulation. It is probable that the majority of the Ischnocera take up the same position in copulation (Sikora and Eichler, 1941), that is the male dorsal surface under the female ventral surface, the male clasping the female either with the antennae or forelegs. The more primitive position of the male genital opening is ventral or ventro-terminal and during copulation the end of the body is recurved so that the genitalia can enter the ventrally placed vulva of the female (Werneck, 1936. Pl. 1); this recurving of the body would obviously be difficult in the short, round-bodied forms, and it is found that in these the genital opening of the male lies on the dorsal surface. This dorsal position of the male genital opening is found in unrelated families and has probably been developed independently more than once. Only one genus (*Labiocotes*) is known of short, round-bodied forms in which the male genital opening is ventral, and it is possible that these take up one of the other positions in copulation as described by Sikora and Eichler (1941). It might happen that in an isolated population of birds the Mallophaga population had occupied the favorable habitat of the head, and the shape of the abdomen became slightly modified; any modification in this region might lead to a difference in mating behavior and hence on the reunion of the louse populations there would be definite preferential mating resulting in the continued isolation of the two populations. The process, of course, may have been reversed: a slightly shortened body form being produced by the random fixation of mutations in a small isolated population; this form would not only be sexually isolated from the parent population, but would be preadapted for the occupation of the head niche.

Sometimes it seems to have happened that in a form in which the male genital opening had moved to the dorsal surface because of the shortening of the abdomen, there was a secondary lengthening of the body. This may be the case in the wing louse (*Columbicola*) of the Columbiformes (Pigeons and Doves), which, unlike other long-bodied forms, has the genital opening on the dorsal surface; it may have become modified for the head niche in isolation, but on the colonization of other host populations found this niche already occupied and was forced to adapt itself to the wing habitat.

(b). The second character which may have played a considerable part in speciation is the sexual dimorphism of the antennae. This character may be found in species belonging to all the families of the Ischnocera; in some genera such as *Degeeriella* from the Falconiformes it has only been found in one species (undescribed), in others such as *Goniodes* from the Galliformes (Game birds) it is present in the majority of species. It is not a generic character and there are instances of two species in which the females are very similar, but the males of one have enlarged and modified antennae.

As the antennae are used to clasp the female during copulation even incipient dimorphism might lead to a difference in mating behavior.

If this character, non-adaptive in its incipient stages, was developed in a small isolated population by random fixation it would probably lead to a difference in mating behavior and, hence, to sexual isolation of this population on reunion with its parent population. When a host species has two sympatric species of an Ischnoceran genus it is commonly found that these differ in the presence or absence of sexual dimorphism of the antennae, or in the degree of sexual dimorphism (table 7). This character may also have been responsible for the formation of species which gave rise to some of the sympatric genera now found on some host orders (table 8). Again the fact that in all the genera of true wing lice (table 1) the majority of species show sexual dimorphism of the antennae, whereas in all the true head lice (table 1) it is rare, suggests that this character may have been the initial isolating factor in the formation of these ecological types. The less common occurrence of sympatric species and genera in the Amblycera may be partly due to the absence of sexual dimorphism of the antennae, which in most species of this superfamily, anyhow, can play no part in mating.

TABLE 7. *Examples of host species parasitized by two related species of Mallophaga, in one of which the antennae are similar in the two sexes and in the other dimorphic*

Starred species show slight sexual dimorphism of the antennae in contrast to the related species in which the male antennae are considerably enlarged

Host species	Mallophaga species: Antennae dimorphic	Mallophaga species: Antennae similar
Tinamiformes (Tinamous)		
Tinamus tao septentrionalis	*Kelloggia mirabilis*	*K. taoi*
Rhyncotus r. rufescens	*Heptapsogaster sexpunctatus*	*H. rotundatus*
Sphenisciformes (Penguins)		
Eudyptes c. crestatus	*Austrogoniodes hamiltoni*	**A. macqueriensis*
Procellariiformes (Petrels)		
Pterodroma m. mollis	*Trabeculus* sp.	*T.* sp.?
Galliformes (Game birds)		
Numida meleagris major	*Goniodes perlatus*	*G. gigas*
Afropavo congensis	*G. chapini*	*G. afropavo*
Arborophila r. rufogularis	*G. processus*	**G. indicus*
Lophortyx californica	*Lagopoecus docophoroides*	*L.* sp. n.
Rallidae (Rails)		
Porphyrio madagascariensis aegyptiacus	*Rallicola* sp?	**R.* sp?
Strigiformes (Owls)		
Bubo b. bubo	*Strigiphilus heteroceras*	*S.* sp?
Passeriformes, Corvidae (Crows)		
Corvus corax lawrencei	*Bruelia* sp?	**Bruelia* sp?

TABLE 8. *Examples of host groups, the members of which are parasitized by two related genera of Mallophaga, in one of which the antennae are similar in the two sexes, and in the other dimorphic*

Starred genera have a few species in which the antennae are similar in the sexes

Host order	Genera of Mallophaga: Antennae dimorphic	Genera of Mallophaga: Antennae similar
Tinamiformes	*Nothocotus* **Heptapsogaster*	*Megaginus* *Discocorpus*
Procellariiformes	*Pseudonirmus*	*Episbates*
Galliformes	**Goniodes* *Chelopistes*	*Goniocotes* *Labiocotes*
Columbae	*Coloceras*	*Campanulotes*

III. Ecological Factors in Mallophaga Speciation

1. Intrinsic changes in each ecological niche

Under this heading are discussed the changes brought about in each habitat type by adaptation to the changes in its particular ecological niche, and which have been mainly responsible for the production of the allopatric genera and species. This is Simpson's "phyletic evolution" (1944, 202) and, as he shows, it consists of changes of populations as a whole, the new species replacing the former species. The processes involved in this mode of evolution differ in no way in the case of the Mallophaga from those of a group of free-living insects.

Once the Mallophaga had been able to adapt themselves to life in general on the body of the bird, the main selecting fac-

tors were, presumably, both interspecific and intraspecific competition and attack by the bird; this latter factor would make the head and neck the most secure place and may have been responsible for the production of the specialized type found on the wings. (Although the head and neck niche is the safest place in respect to preening by the host, it may have certain disadvantages in some birds; a sparse covering or the complete absence of feathers might make this niche uninhabitable in hot, dry climates, or on those birds which spend much time under water.) It seems probable that it is in these two habitats, that of the head and of the wing, that competition is the most severe, as the Mallophaga of these niches have developed the most extreme specialization of the head to the feather structure of the particular host. The production of a new species by a change of the whole population through adaptation to a changing environment is dependant mainly on the selection pressure, which here must have been competition between the Mallophaga. Chandler (1914) has shown that the minute structure of the feather is usually an ordinal character, and it is, therefore, of interest that the specialized head lice and the similarly specialized wing lice are divisible into genera, each of which is restricted to an order of birds (table 1); there are certain exceptions to this (table 3), the reasons for which will be discussed below. Further three host groups, the Momotidae (Motmots), Meropidae (Bee-eaters) and Rhamphastidae (Toucans) which have genera (*Bruelia* and *Menacanthus*) of less specialized lice also found on the Passeriformes, each have a specialized head louse different from that of the latter order (table 1). Such genera, restricted to certain orders of birds, show differences in the characters of the head framework and sutures which give support and mobility, and which, presumably, allow the most efficient application of the mandibles and of the *pulvinus* (*sens.* Cope, 1940, 120) [which serves an important function in feeding and holding to the particular feather structure of the host order concerned.

The chief factor, therefore, influencing the production of the allopatric species and genera of the Mallophaga has been the successive splitting of the host populations during the evolution of the birds, thus leaving isolated louse populations. Within these isolated "islands" each ecological type diverged from those on other "islands" by specialization for the changing environment of its own niche and by the random fixation of non-adaptive characters made possible by the isolation. Within an order of birds the environmental differences between the same ecological niche are, in general, slight, and this has led to any one genus of parasite confined to an order of birds having a large number of allopatric species, one on each host species (tables 4 and 5) or one on a group of related host species (table 6); in the case of some of the Tinamidae, an ancient group of birds where presumably the louse populations have been isolated for a greater time, different species or subspecies of lice are found on the subspecies of a polytypic host species (table 4). These allopatric species do not usually differ greatly from each other, and are separable mainly on the characters of the external sclerotization and measurements (probably correlated with feather texture and feather size) and on nonadaptive characters such as the male genitalia. Such species are comparable to those allopatric species of a genus of free-living animals found on continental islands and in other isolated habitats.

2. Change of ecological niche on the same host species

Although any one host species may have a number of genera and species of Mallophaga recorded from it, any individual bird does not necessarily have them all. As shown above, a louse species may become extinct throughout parts of its host's range; this would mean that one of the ecological niches would be empty of

its specialized louse type, and might, especially if it was such a favourable niche as the head, be occupied by another species which would become secondarily adapted to the new habitat. This seems to have happened in the head niche of the Sturnidae or starlings: in this family the specialized head louse, *Philopterus*, characteristic of the suborder Passeres (Song birds), is absent, but the starlings have a genus *Sturnidoecus* (fig. 2d) which superficially resembles *Philopterus* (fig. 2e). *Sturnidoecus* has the large head with the complicated arrangement of sutures and sclerotization, and the short, round abdomen characteristic of the occupants of the head niche. But the characters of the female genital region, the shape of the alimentary canal, the internal male genitalia and spermatheca show that it is more closely related to another genus *Bruelia* (fig. 2b) also found on the Passeres, which has the smaller head and more elongate body form. The fact that the genus *Sturnidoecus* has also been found on species of *Passer* (Ploceidae) and *Turdus* (Turdidae) in various parts of the world lends support to the theory of secondary interspecific infestations discussed below. It seems probable in these cases that populations of the *Passer* and *Turdus* species concerned, lacking the head louse, became secondarily infested by *Sturnidoecus* from one of the Sturni-

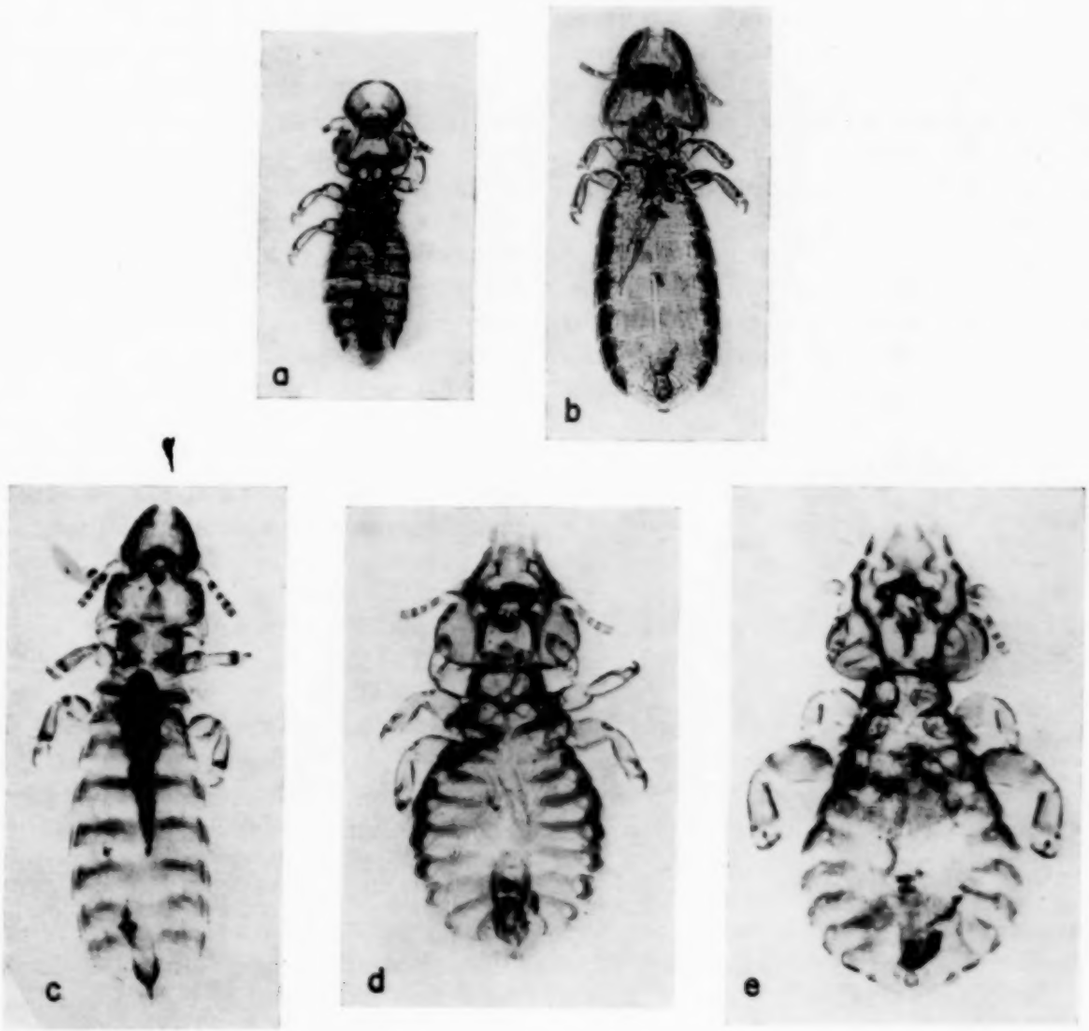

FIG. 2. Mallophaga of the Passeriformes. a. *Bruelia biguttata*. × 35. b. *B. daumae*. × 35. c. *B. nebulosa*. × 65. d. *Sturnidoecus sturni*. × 56.5. e. *Philopterus* sp. × 60.

dae, and these in the absence of competition were able to establish themselves on the head. *Sturnidoecus*, unlike true *Philopterus*, is not so closely restricted to the head and may be found on other parts of the body.

IV. The Origin of Sympatric Species

1. *Sympatric speciation.*—At first sight this would seem to be the most likely explanation of the presence of closely related species and genera found in a restricted and isolated geographical area. Mayr (1947) has summarized the arguments against the theory of sympatric speciation in general and these need not be repeated. In the case of the present group it seems unlikely, in the light of modern knowledge of genetics, that speciation could have taken place in an area such as the external body surface of a bird where there are no extrinsic isolating barriers, the plumage of one area grading into the next or in close contact with it. Even if the theory of conditioning is accepted, so that the Mallophaga hatched on the head and neck would tend to remain in that area, there would seem to be nothing to prevent interbreeding between individuals on the neck and those conditioned for the adjacent zone of the back and wings; such interbreeding would ensure the maintenance of gene flow between the two populations. However, the non-uniform distribution of plumules found in some orders might form isolated areas for populations conditioned to this type of feather, analogous to the isolation of free-living populations by intervening desert areas. If this feature had been responsible for speciation it would be expected that those orders in which there is a uniform distribution of plumules would have fewer sympatric genera. Only two examples of such orders need be taken to show that this is not so: the Procellariiformes (Petrels) which have ten Ischnoceran genera, some of which are divisible into two or more species-groups found on the same host, and the Falconiformes (Birds of Prey) which have four Ischnoceran genera. Finally the available evidence suggests that the problem can be explained by the process of speciation through geographical isolation.

2. *Isolation.*—It has already been shown under section II, 3 and 4 how the isolation of parts of the louse populations of a host species and their subsequent reunion may have been responsible for some of the sympatric species now found on one host.

3. *Secondary interspecific infestations.*—Host specificity which may prevent the establishment of a louse transferred to a host of a different species has been discussed above; it was shown that although, in general, the Mallophaga are host specific there are cases of immigrant parasite species establishing themselves on a new host. It can also be presumed that establishment on a new host was more possible at a time in the evolution of the louse before it had developed extreme host specificity and when the hosts themselves, less divergent during the earlier stages of their evolution, offered a more uniform environment. This colonization of a new host by a species of Mallophaga is analagous to the trans-oceanic colonization of oceanic islands by free-living animals, and, as in this latter case, may have contributed to the presence of sympatric species and genera in the parasite. There is some evidence in support of this supposition. Eichler (1942, 78) has drawn attention to the fact that those orders of birds which are represented by a small number of species are those which have one, rarely two genera of Mallophaga, while those with many species usually support a number of sympatric genera and species (table 9). Although, in general, this statement is correct there are a number of exceptions which must be considered, as well as possible alternative explanations to that of secondary infestation as the cause. Some orders of birds now represented by a few species are, presumably, the relics of once numerous and widely spread groups. As

TABLE 9. *Number of species in each host group with the number of sympatric genera and species-groups of Mallophaga*

Host group	Number of species in group	Number of Mallophaga genera and species groups
Struthioniformes (Ostriches)	1	1
Rheiformes (Rheas)	2	2
Apterygiformes	3	2
Casuariiformes (Cassowaries)	3	1
Gaviiformes (Loons)	4	2
Coliiformes (Colies)	6	2
Phoeniculidae (Wood-hoopoes)	6	2
Pterocletes (Sand-grouse)	16	2
Sphenisciformes (Penguins)	17	2
Colymbiformes (Grebes)	20	2
Musophagi	20	5
Tinamiformes	32	21
Bucerotidae (Hornbills)	46	7
Pelecaniformes	54	6
Apodi (Swifts)	77	2
Alcedinidae (Kingfishers)	87	2
Caprimulgiformes (Goatsuckers)	92	2
Procellariiformes	93	15
Ciconiiformes	111	10
Cuculi	127	7
Strigiformes	134	3
Anseriformes	148	7
Galliformes	241	19
Falconiformes	271	9
Columbae	300	10
Charadriiformes	308	10
Psittaciformes (Parrots)	315	7
Passeriformes	5093	11

The Phoenicopteridae are omitted from the Ciconiiformes as their Mallophaga in no way resemble those of this order. For the same reason the family Opisthocomidae (Hoazin) is omitted from the Galliformes. The whole of the Gruiformes and certain other orders are omitted for reasons given in the text under "Note on Tables." The Todidae, Leptosomatidae, Galbulidae, and Bucconidae are omitted as no Mallophaga have been seen from these groups. Although all the genera and species-groups given will not be found on all the bird species throughout the order, an attempt has been made to list only those which could be sympatric; thus *Bizarrifrons* is not included in the number of genera found on the Passeriformes as it is the allopatric replacement of *Sturnidoecus* on the Icteridae (Troupials)

already shown any one species or genus of Mallophaga is not necessarily found throughout the range of its hosts; for instance, *Piagetiella*, which lives in the gular pouch of the Pelecaniformes, has been recorded amongst the Phalacrocoracidae (Cormorants) only in the New World and Antarctic species. It follows therefore, that the extinction of many genera and species of an order of birds may result in the fortuitous extinction of some of the genera of Mallophaga normally found on the order.

Many of the orders of birds now represented by a few species are those in which the feather covering is of a uniform and homogeneous character, Struthioniformes, Rheiformes, Casuariiformes, Apterygiformes, and Sphenisciformes. On these birds there will be no well differentiated ecological niches and this will limit the number of ecological types of Mallophaga and hence the number of genera. If such a homogeneous feather covering is primitive (Lowe, 1928) then it is probable that the members of these bird orders never had more than a few genera of Mallophaga, or if secondary, then the extreme ecological types might have been eliminated with the degeneration of the feathers. In the case of the Tinamiformes, a primitive order but without the homogeneous feather covering found in the bird orders mentioned above, the number of sympatric genera and species of Mallophaga is the highest known, although the number of host species is not large (table 9). However fossil Tinamous, belonging to the modern family Tinamidae, are known from the Pliocene of S. America, and it is probable that this family was represented by a greater number of species between the time that it lost its primitive homogeneous feather covering and the present day. In addition its later evolution has taken place within one continent, the genera are well defined, most of the species are represented by many subspecies and many of the species are sympatric. During the long evolution of this family, then, there must have been ample opportunity for the interchange of lice between the host forms at all stages of differentiation; this may explain, at least in part, the unusually large number of sympatric genera and species of Mallophaga found in the Tinamiformes.

The unusually large number of genera and species of Mallophaga found on some bird orders may also be due to the individual birds being able to support a greater number of parasites. Features of the feather covering or physiological characters of the body may provide a greater number of ecological niches and, in general, make the body of these birds a more

favorable habitat for the lice, resulting in a greater number of immigrant lice being able to establish themselves. The opportunities for the transference of lice between different host species should also be taken into account—both the Tinamiformes and Galliformes which show a high number of sympatric genera and species are birds which make frequent use of dust baths, a method of lice transference already mentioned.

Those bird orders with a large number of species but with few genera of Mallophaga (table 9) may, in contrast to those above, either have a feather covering which gives few ecological niches (already discussed under the primitive orders), or the body may in general be unsuitable as a habitat for lice, so that their survival has always been precarious, resulting in the frequent extinction of forms and the infrequent establishment of immigrant lice.

In spite of the reservations discussed above it would seem that the presence of at least some of the sympatric genera found on any one order of birds may have been brought about by the interchange of lice populations between different members of a bird order, after the former had diverged sufficiently to prevent interbreeding. The factors, already discussed, such as the preadaptation for a certain niche by the immigrant louse population, the necessity of the absence of competition in that niche, or the presence of competition which might force the species, partly adapted for one niche, into another, would all affect speciation. The advantages of interspecific exchange of lice populations over intraspecific is that the two lice populations, having usually diverged to a greater extent, are more likely to be reproductively isolated.

Apart from secondary infestations by louse populations within one host order where it would be expected that environmental conditions and host specificity would not be strongly preventive factors, there has probably also been a number of cases of a louse species establishing itself on a host of another bird order. The presence of one species of *Perineus* (a genus elsewhere restricted to the Procellariiformes and related to other genera on that host order) on several species of the bird family Stercorariidae (Skuas) of the order Charadriiformes, must be a case of a relatively recent colonization of a new host. In this case the louse has become specifically but not generically distinct from those on its original host order, but where this type of colonization took place at an earlier stage in evolution divergence might have proceded further, and the two lines would now be included in higher categories, each having given rise to one or more genera differentiated and specialized for each host order. It is possible that some of the inexplicable cases of distribution and relationships of the Mallophaga are due to this cause. The widespread occurrence of the genus *Saemundssonia* (which probably originated on the Charadriiformes) on the Procellariiformes may also be another case of a comparatively recent secondary infestation. This example of two genera common to the Procellariiformes and Charadriiformes, together with species of Amblycera on the two host orders which are either related or superficially alike, suggests that the environment provided by the Procellariformes and Charadriiformes may be similar (perhaps due to the specialization of superficial characters to a similar environment) and that this has made a limited exchange of lice between the two host orders possible.

Further evidence that the origin of sympatric species may be traced to secondary infestations is provided by the present distribution of certain species. An analysis of the distribution of the species of a genus of Mallophaga parasitic on a group of related birds shows that, in general, each bird species or group or related species has one louse species peculiar to it; in addition some of the host species may have a second sympatric species which is also found on another, but not closely related, species

of the host group in question. An example of this is found in the species of *Quadraceps* parasitic on the Sterninae (Terns): *Sterna paradisaea, S. hirundo* and *Chlidonias nigra* each have a distinct species of *Quadraceps;* but the species normal to *Chlidonias nigra* may also be found, occasionally, but apparently established, on *Sterna hirundo*. This suggests that the latter species has become established on a new host and may be found living normally together with the indigenous species. In other instances it may actually take the place of the original species; this would explain such cases as the occurrence of the same species of *Saemundssonia* on the two, not closely related, host species, *Sterna hirundo* and *Gelochelidon nilotica* (see Clay, 1948, 142).

Perhaps some mention should be made of the possible role in speciation played by phoresy. There are now (Thompson, 1937; Clay and Meinertzhagen, 1943) a considerable number of records of flies of the family Hippoboscidae (themselves parasitic on birds) being found with Ischnoceran Mallophaga attached. It is possible that transference by Hippoboscid flies is one of the normal ways in which the cuckoo obtains its louse population, as, except during copulation, there is no contact between individual cuckoos. The flies frequently carry more than one louse: two specimens of *Ornithomyia avicularia* recently taken from a young blackbird (*Turdus merula*) in England had respectively three males and one female, and one male and four females of *Bruelia merulensis* attached to the abdomens. Either of these batches taken to a new host could have given rise to a new louse population. At other times single specimens may be carried; if a fertilized female, bearing a character of an incipient isolating mechanism, was transferred to an individual of a louseless host population (of the type discussed above), it might give rise to a population in which this character, merely by the process of genetic drift, would become established and thus reproductively isolate this population if the hosts were later recolonized by the original parent population. It may be relevant that the Amblycera, showing fewer sympatric genera and species, have never been recorded attached to Hippoboscid flies.

V. Causes of Anomalous Distribution

In conclusion it may be useful to summarize the causes for cases of anomalous distribution of genera and species found in the Mallophaga:

1. Related species of Mallophaga found on unrelated hosts may be descendants of a common ancestor evolved before the bird groups in question were separated, and which have remained relatively unchanged since. Examples of this type of genus (table 2) probably either belong to the less specialized Amblycera or to those Ischnocera (fig. 1d) which have not developed the modified head specialized for the particular feather structure of a host group. Extinction in most bird orders would explain their present discontinuous distribution.

2. Such species may be descendants of unrelated forms which have acquired similar characters in response to a similar environment. Although the cases of such convergence which misled the earlier workers on Mallophaga have now been recognized as such, it is a cause which should be considered in any case of apparent anomalous distribution of a genus. There is no doubt that many of the families as now recognized contain genera which are not related, but resemble each other through adaptation to the same ecological niche on different bird orders. In the Heptapsogastridae, a family of the Ischnocera found on the Tinamiformes, the genera have assumed a superficial resemblance to the different ecological types found on other orders of birds (information on the habitats occupied by most of the genera of the Heptapsogastridae is unfortunately not available). The Heptapsogastridae are an interesting example of adaptive radiation in one family which

became the chief occupants of a territory where there was probably little competition.

3. The species may be descendants of a common ancestor which have evolved on similar lines, that is parallel evolution. The term "parallel evolution" is used here for the evolution of the descendants of a common ancestor which, although divided into isolated populations, evolved on similar lines resulting from the identical mutations of identical genes; and because of the similarity of the environment in any one ecological niche, these genes would have similar selective values and produce a similar phenotype. Some of the cases of apparently anomolous distribution and relationships of Mallophagan genera may be explained on similar lines to those suggested by Wood (1937 and 1947) for the rodents. All the Ischnocera are basically rather similar in both their internal and external anatomy—it seems doubtful whether the hundred or more Ischnoceran genera should be divided into more than four or five families. The characters common to all the Ischnocera were probably the result of an early and rapid period of evolution specializing them for life on the bird; these initial modifications (as Wood, 1947, suggests in the case of the rodents) would largely predetermine the direction of further evolution, so that within each of the four or five families the possible mutations would tend to be the same and to have the same survival value when subjected to a similar environment. The Ischnocera are a most successful group which have branched out into a great many lines occupying the different ecological niches on the body of the bird. There is in this group a genetic predisposition towards increased mobility and strengthening of the parts of the head capsule by the formation of secondary sutures and lines of thickening, and in many cases these seem to have developed on parallel lines. Such specialization can be seen within the genus *Bruelia*, where there is an almost complete transition from the unmodified circumfasciate head (e.g., *B. biguttata*, fig. 2a), through the species with partially interrupted anterior margin (e.g., *B. nebulosa*, fig. 2c), to those with well marked anterior sutures and "signature" (e.g., *B. daumae*, fig. 2b); the extreme form of this development is seen in the related genus *Sturnidoecus* (fig. 2d). On most orders of birds there are one or more genera (e.g., *Degeeriella* (fig. 1b), *Cuculicola* and *Picicola*) which have never developed the more specialized head and are, therefore, naturally more similar to each other than are the forms with specialized heads, although not necessarily more closely related.

Parallel evolution on the above lines may have been responsible for the *Rallicola*-complex (table 3a) found on hosts belonging to many orders; as these species show specialization of the head it seems unlikely that they are the unchanged descendants of an ancestor developed in this form before the Apterygiformes had split off from the main stem of the evolving birds. The diagnostic characters of this group of species are the presence of spine-bearing tubercles each side of the female genital region and the general characters of the male genitalia. *Bruelia* found on the Passeriformes is also related to this group—there are species of *Bruelia* which are only separable from *"Furnaricola"* (table 3a) by the absence of the spine-bearing tubercle and characters of the male genitalia. It is possible therefore that the whole of this complex of genera is descended from a stock which had this genetic predisposition of the head to develop its secondary sutures and thickening on certain lines and to the formation of the spine-bearing tubercles. This might mean that both *Bruelia* and *Furnaricola* developed from a common ancestor on the Passeriformes, the spine-bearing tubercles being lost or never developed in the former genus. *"Furnaricola"* then, although generically indistinguishable from *Rallicola*, would be phylogenetically more closely related to *Bruelia* and its related genus *Sturnidoecus*. It

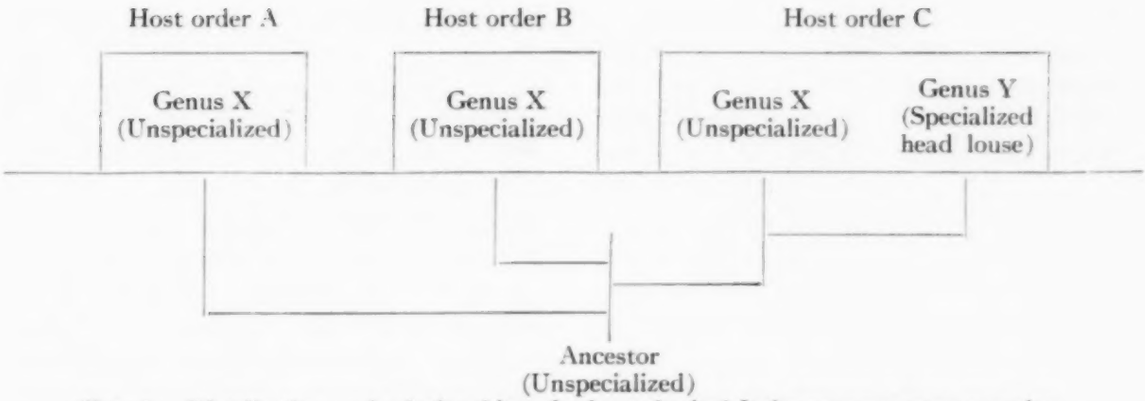

FIG. 3. Distribution and relationships of a hypothetical Ischnoceran genera complex.

seems likely that this type of parallel evolution has taken place more than once in the evolution of the Ischnocera, and is one of the likely sources of error in the formulation of a natural classification. Another source of error may be found among the unspecialized Ischnocera (table 2). Such a complex of genera and species-groups as *Degeeriella*, for instance, probably contains the relatively unchanged descendants of an ancestral stock which gave rise to the species now found on the different host orders; but on some orders such an ancestral stock may also have given rise to the specialized head or wing lice, either because these niches were empty through secondary absence, or because it is the case that all the Ischnoceran genera found on one bird order are derived from a common ancestor on that order. A hypothetical case of such relationships is shown in figure 3. It is difficult to demonstrate in a linear system the natural relationships between such groups of species (fig. 3, genus x) which are generically indistinguishable although from different host orders, and another group of species (fig. 3, genus y) derived from a common ancestor of (and hence more closely related to) one of the former groups on one of the host orders concerned; this derived group, because it occupies a different ecological niche, may now be so distinct that it is usually placed in a different family. The only method available to represent the actual phylogenetic relationships is either to split up the species-groups from the different host orders into genera, which is often virtualy impossible because of the overlap of characters; or to include the whole complex (genus x and y) in one genus, although apart from the characters shared by the family, they may have few others in common. Such a classification although phylogenetically correct soon ceases to be a convenient one.

Hopkins (1943, 16) has also emphasized the difficulties in the generic classification of the Trichodectidae (Mallophaga) of mammals caused by the amount of parallelism which has apparently taken place in their evolution.

4. That the species are descendants of an ancestor which became established on another host order by secondary infestation; this has been discussed above, and is the most likely explanation of the example in table 3, b.

5. Human error in the evaluation of the systematic position both of the host and parasite must be taken into account. This may be the explanation of the classic case of the Phoenicopteridae (flamingoes), usually placed with the Ciconiiformes, which have three genera of Mallophaga found elsewhere only on the Anseriformes (table 3, e, f, g); this distribution supports the inclusion of the flamingoes in the latter order instead of in the Ciconiiformes. It may also explain the genera common to the Galliformes and the Musophagi (table 3, d, Clay, 1947 (2)). It is of course not always possible to dis-

tinguish the cases caused by secondary infestations from those due to incorrect classification of the hosts, but, as Hopkins (142, 100) suggests, the number of species involved serves as a clue to the cause. The case of the Gruidae with one genus also found on the Charadriiformes (table 3, b) and three distinctive genera of its own, does not suggest any relationship between the Gruidae and the Charadriiformes; whereas the three genera common to the Phoenicopteridae and the Anseriformes suggest that the affinities in this family lie with the latter order. An example where the Mallophaga give no conclusive evidence of the affinities of the host is *Aramus:* this genus, usually placed with the Gruiformes, has one genus of Mallophaga also found on the Ciconiiformes (table 3, c), and two (*Rallicola* and *Pseudomenopon*) also found on the Rallidae, and one (*Laemobothrion*) found on a number of host groups, including the Rallidae and Ciconiiformes.

The above paragraphs deal with the anomalous distribution of genera, but it may also be of interest to mention briefly the distribution and relationships of the species within a genus of Mallophaga restricted to one host group. As in the case of the genera, and as is inherent in this theory of their evolution, the relationships between the species of Mallophaga reflect those of their hosts (table 4–6). The degree of difference between related species of Mallophaga will be dependent not only on their own age and plasticity, but on the differences in their environments which are formed by the external characters of their hosts species; the latter differences being dependent on age, plasticity and environment of the host species. There are three factors which may confuse the normal relation between classification of host and parasite: *Convergence.* A particular character of the feather covering found in a number of not closely related birds, which is due to convergence and not, therefore, of phylogenetic importance, may be reflected in the species of Mallophaga found on the hosts concerned. In the genus *Philopterus* parasitic on the Passeriformes, for instance, a certain type of thickening of the anterior margin of the head and framework supporting the mouth parts has been developed in species from hosts belonging to different families; the available evidence suggests that this is a modification in response to feathers showing iridescence and hence a different physical structure. *Sympatric pairs.* Three related host species, x, y, z, may have been parasitized by three pairs of sympatric species, a^1 and b^1 on host x, a^2 and b^2 on y,

Host species	x		y		z	
Parasite species	a^1	(b^1)	(a^2)	b^2	a^3	(b^3)

FIG. 4. False deduction of host relationships through the extinction or ignorance of some of the sympatric species. All the parasite species belong to the same genus. Those in brackets are now extinct or unknown. a^{1-3} and b^{1-3} are, respectively, closely related allopatric species.

and a^3 and b^3 on z (fig. 4); species a^{1-3} and species b^{1-3} are, respectively, closely related allopatric species. If some of these species become extinct (or have not been collected) so that host species x appears to have only parasite species a^1, and y to have only b^2 and z only a^3 (fig. 4); then, from a consideration of the parasites, host species x and z will appear to be more closely related to each other than either is to y because the parasite species a^1 and a^3 are in fact more closely related to each other than to b^2. *Secondary infestations.* This has already been discussed above, and it was shown that the occurrence of a species of *Saemundssonia* common to the two terns, *Sterna hirundo* and *Gelochelidon nilotica,* did not necessarily mean close relationship between the two hosts, but could be explained as a case of secondary infestation.

These many cases of anomalous distribution of both genera and species show clearly that the phylogenetic relationships of the Mallophaga cannot be used as in-

fallible evidence of the phylogenetic relationships of the hosts as is implied by some writers on the subject. The relationships of the parasites must be considered as useful sources of contributory evidence in elucidating the systematic position of birds of doubtful affinities, but such evidence must be interpreted in the light of the above discussion and assessed together with fossil, morphological, and biological evidence of the birds themselves.

Conclusions

It has been shown that in the particular case of a group of obligate ectoparasites speciation can be explained by the normal process of geographical isolation; and that factors similar to the formation of the populations of continental islands, the colonization of oceanic islands and the isolation and reunion of populations—which have contributed to speciation in free-living animals—have acted likewise in the evolution of the Mallophaga, if host distribution is equated with geographical distribution. It should be emphasized that the birds themselves underwent a rapid period of evolution: by the Upper Eocene most of the modern families were established; this was followed by a period of little morphological change so that Miocene birds, for example, can often be assigned to modern genera (Howard, 1947). During this period of rapid evolution the lice populations must have been subjected to conditions of great evolutionary stimulus. Not only had the ancestral louse colonized a new and empty habitat, but this was constantly being modified by the evolution of the birds. The louse populations were frequently being divided into many partially isolated local populations—through the isolation of their hosts and through the extinction of louse populations in parts of the range of their hosts; and this, as emphasized by Sewall Wright (1945, 416), has been one of the factors responsible for rapidity of evolution. It is probable that by the Upper Eocene, when most of the modern bird families were established, the majority of the genera of Mallophaga had been established, and as the evolution of the birds slowed down, and thus lessened the stimulus, so also did that of the lice. The lice living in a more constant environment than their hosts have, during that time, probably changed to a lesser extent than the latter; this being reflected in the many cases of a genus of Mallophaga being restricted to one order of birds. The course of evolution and the present distribution of the Mallophaga supports "the evolutionary role of accident" (Mayr, 1947, 271). The apparently successful occupation of most of the available niches —including the inside of the shafts of the wing feathers on some birds and the gular pouch of the Pelecaniformes—on such a small area as the body of a bird can be explained by the normal process of natural selection: a louse arriving on a new host, if it is unable to compete with the established population, must either occupy an empty ecological niche or face extinction; this latter fate was presumably frequent.

It has not been possible to include in a paper of this kind all the available evidence for some of the statements made; much of this evidence will be included in a paper now in the course of preparation. The criticism may be made that there is as yet insufficient knowledge of the group as a whole on which to base the arguments used here; this is partly true, but it is hoped that such a paper will encourage further work on the biology and morphology of the Mallophaga. Further, any worker attempting a natural classification of this difficult group is forced to formulate some conception of its evolution, without which the classification will become even further divorced from a natural representation of relationships than it is at the moment.

Note on Tables

It has not been possible to reduce the data given in the tables to a numerical form because there are still a very large number of birds in most orders of which the Mallophaga are not fully known; the tables, therefore, contain only examples of the points mentioned in the text.

It is considered that these examples, which have been taken from a wide range of hosts and Mallophaga, support the general arguments used, and suggest that as further information becomes available it will not be greatly at variance with such examples.

Some difficulty arises over the category of host group to be used. Although, in general, the genera of Mallophaga follow the orders of birds, as usually arranged (Wetmore, 1940), this is not invariably the case. There are suborders or families of birds, the Mallophaga of which are quite different from those of the rest of the order (examples of these have been mentioned above); where the inclusion of these would affect the argument (as in table 9) they are omitted. In the Gruiformes, the families fall into at least six groups, each of which have distinctive genera of Mallophaga; in this case the suborder or family of which the Mallophaga form a related group is used. The Mallophaga of the Trochili (hummingbirds) and of all the orders (with the exceptions given in table 9) from the Trogoniformes to and including the Passeriformes (Wetmore, 1940, 8–11) suggest that these orders should be considered as a single complex; except for the Passeriformes, therefore, they have been omitted from table 9 as being misleading.

Acknowledgments

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Summary

1. The Mallophaga, a group of obligate ectoparasitic insects found on birds and mammals, may have a large number of genera and species occurring on one host species. In a group of related host species, each species may have allopatric species of a number of sympatric genera of Mallophaga common to the group, and, in addition, sympatric species of these genera.

2. During their evolution, the Mallophaga branched out to fill the different ecological niches found on the body of the host, and for which they became specialized. The occupant of each niche has changed with the changing environment of its particular niche caused by the evolution of the hosts themselves.

3. Host isolation, the equivalent of geographical isolation, may explain speciation in the Mallophaga. Factors which have been responsible for the isolation of louse populations are: 1. The divisions of their host populations into non-breeding units —forming new species of hosts which diverged into the families and orders now known; the isolated louse populations thus formed diverged from each other and became specialized for the new characters developed by their respective hosts. This type of speciation is analogous to that on continental islands formed by the disappearance of land connections. 2. The development of host specificity; this would increase the isolation of the populations of any one host species. 3. The temporary isolation of parts of a louse population by the temporary isolation of parts of its host population, or by the extinction of a louse species in part of its host's range, thus isolating the two populations on each side. If these periods of isolation were sufficient to enable the development of some sexually isolating mechanism in one of the isolated populations a new species would be formed.

4. The ecological factors influencing the speciation in Mallophaga have been the intrinsic changes in each ecological niche and the migration of a species from one niche to another on the same host. These factors have affected mainly the proportions of the body and the secondary thickening and sutures of the head, which are important characters in feeding and in clinging to the feathers or hairs of the host.

5. The frequent occurrence of sympatric genera and species on any one host species may be explained by the isolation and later reunion of parts of a louse population as discussed under 4; and by secondary interspecific infestations.

6. Although in general the relationships of the Mallophaga reflect those of their

hosts, these basic relationships have now become confused, and the many cases of anomalous distribution make it impossible to use the evidence from the Mallophaga as an infallible guide to the phylogeny of the host. The factors responsible for these cases of anomalous distribution are discontinuous distribution, excessive convergent and parallel evolution making a reliable evaluation of phylogenetic relationships difficult, and secondary interspecific infestations.

7. In conclusion it is possible to say, if the host distribution of these parasites is equated with the geographical distribution of free-living animals, that the same general factors have been responsible for speciation in both cases.

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THE *WILLISTONI* GROUP OF SIBLING SPECIES OF *DROSOPHILA*

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Introduction

Species in sexual cross-fertilizing organisms are reproductively isolated populations. Such populations may or may not be distinguishable in morphological characteristics. Mayr (1942) has proposed the designation "sibling species" for species that are morphologically similar or identical. Camp and Gilly (1943) have called such species phenons, and other authors have referred to them as physiological species (Lancefield, 1929), cryptic species, etc. The theoretical interest of sibling species lies in that their existence shows that reproductive isolation may arise without divergence in morphological traits, and that physiological differences are not necessarily accompanied by morphological ones.

As disclosed especially by the work of J. T. Patterson and his school, the genus Drosophila contains several groups of closely related species with small morphological differences between them. The present article reports the results of a study of a cluster of four sibling species native to tropical America, that previously have been confused under the name of *Drosophila willistoni* Sturtevant.

Drosophila willistoni *Sturtevant and* Drosophila paulistorum *Dobzhansky and Pavan, sp.n.*

In 1896, Williston described *Drosophila pallida*, a species from the isle of St. Vincent, in the West Indies. The name being preoccupied, Sturtevant changed it in 1916 to *willistoni*. Sturtevant (1921) and Patterson (1943) recorded this species from a fair number of localities in a territory extending from the Bahamas, Florida, Cuba, and Mexico, through the West Indies and Central America to Brazil.

In 1943, Dobzhansky and Pavan examined a series of cultures of *willistoni*-like flies descended from progenitors captured in the state of São Paulo, Brazil. These cultures fell into two classes, the flies in some cultures being larger than those in others. A more detailed examination revealed other minor morphological differences between the large-bodied and the small-bodied flies, and an examination of the salivary gland chromosomes suggested that these were different as well. This led to the inference that two distinct although morphologically very similar species were involved, one of them being *willistoni* Sturtevant and the other a new one, to which the name *paulista* Dobzhansky and Pavan was given. Since neither living nor preserved material from outside Brazil was available to Dobzhansky and Pavan in 1943, they conjectured that the species found more frequently among their cultures, which happened to be the small-bodied species, corresponded to *willistoni*, while the less frequent species was a new one, to which the name *paulista* was assigned. We now believe that this conjecture was an unfortunate one.

Through the courtesy of Professor J. T. Patterson, we received a culture of *willistoni*-like flies from Quirigua, Guatemala, and Professor John A. Moore kindly collected several strains for us at Axtla, in the state of San Luis Potosí, Mexico. These strains proved to inter-

[1] Contribution No. 3 of the cooperative research project of the University of São Paulo and Columbia University on genetics and ecology of tropical *Drosophila*. This work has been supported by grants from the University of São Paulo, the Rockefeller Foundation, and the Carnegie Institution of Washington.

cross freely with the larger-bodied flies from Brazil. If the species described by Williston from the Isle of St. Vincent is identical with that found in Mexico and Guatemala, a nomenclatorial confusion must be faced, because, in accordance with the Rules of Nomenclature, the name *willistoni* Sturtevant would necessarily apply to the large-bodied Brazilian species to which the name *paulista* was given by Dobzhansky and Pavan. The name *paulista* would thus become a synonym of *willistoni*. The smaller Brazilian species, designated as *willistoni* by Dobzhansky and Pavan, would then require a new name.

The situation can not, however, be definitively settled without examination of living material from St. Vincent and of Williston's types, which are preserved in the British Museum. We have been unable to examine either, and there is no immediate prospect of our doing so; furthermore, it may not be possible from examination of Williston's long-dried specimens to decide which of the four sibling species (see below) they represent. Under the circumstances, we are adopting the following course as temporary expedient that reduces to a minimum the confusion in the existing literature. The name *willistoni* Sturtevant is applied to the larger of the two species found in the state of São Paulo. It is identical with that known to live in Guatemala and in Mexico (the *willistoni* of Patterson, 1943; Patterson and Mainland, 1944; Dobzhansky and Mayr, 1944; and Dobzhansky, 1946; but not of Dobzhansky and Pavan, 1943). For the smaller of the two species found in the state of São Paulo, to which, apparently erroneously, the name *willistoni* was applied by Dobzhansky and Pavan (1943), the name *paulistorum* is hereby proposed.

Drosophila paulistorum *Dobzhansky and Pavan, species nova*

Body smaller than in *Drosophila willistoni* Sturtevant, wings shorter, costal index lower, 4th vein and 5 × indices higher, branches in the arista fewer, width of the front between the eyes greater. The base of the middle orbital bristle only a little posterior and very close to the base of the first orbital.

Type locality: Mogi das Cruzes, state of São Paulo, Brazil.

Type in the Departamento de Zoologia of the Museum of São Paulo.

Ten strains of *paulistorum* from Mogi das Cruzes, in the state of São Paulo, and nine strains of *willistoni*, from the same locality, have been identified by their salivary gland chromosomes, as described below. Five females and five males were taken from each strain, and the length of the body, wing length, costal index, 4th vein index, and 5 × index were measured and the number of branches in the arista counted. The flies measured were raised under optimal feeding and temperature conditions. The body length was measured as the sum of the distances from the antenna to the base of a halter and thence to the end of the anal tubercle. The data are summarized in table 1. It can be

TABLE 1. *Comparison of certain traits in* Drosophila paulistorum *sp. n. and* Drosophila willistoni *Sturtevant*

Trait	Species	M ±m	Limits
Body-length (mm.)	*paulistorum* ♀	2.44 ±0.02	2.00–2.70
Body-length (mm.)	*willistoni* ♀	2.65 ±0.02	2.20–3.00
Body-length (mm.)	*paulistorum* ♂	2.10 ±0.014	1.85–2.30
Body-length (mm.)	*willistoni* ♂	2.18 ±0.015	2.00–2.40
Wing-length (mm.)	*paulistorum* ♀	2.27 ±0.013	2.10–2.40
Wing-length (mm.)	*willistoni* ♀	2.47 ±0.013	2.30–2.60
Wing-length (mm.)	*paulistorum* ♂	2.01 ±0.013	1.80–2.20
Wing-length (mm.)	*willistoni* ♂	2.15 ±0.012	2.00–2.35
Costal index	*paulistorum* ♀	2.01 ±0.02	1.80–2.25
Costal index	*willistoni* ♀	2.12 ±0.02	2.00–2.35
Costal index	*paulistorum* ♂	1.87 ±0.02	1.70–2.10
Costal index	*willistoni* ♂	2.00 ±0.02	1.90–2.15
4th vein index	*paulistorum* ♀	2.03 ±0.02	1.80–2.30
4th vein index	*willistoni* ♀	1.92 ±0.02	1.60–2.20
4th vein index	*paulistorum* ♂	1.93 ±0.02	1.70–2.10
4th vein index	*willistoni* ♂	1.90 ±0.02	1.65–2.40
5 × index	*paulistorum* ♀	2.01 ±0.03	1.70–2.25
5 × index	*willistoni* ♀	1.78 ±0.03	1.55–2.10
5 × index	*paulistorum* ♂	1.90 ±0.03	1.65–2.30
5 × index	*willistoni* ♂	1.88 ±0.03	1.65–2.35
Branches of arista	*paulistorum* ♀	10.66 ±0.08	10–12
Branches of arista	*willistoni* ♀	11.51 ±0.07	10–12

seen that *paulistorum* has a smaller body, a shorter wing, lower costal index, higher 4th vein and 5 × indices, and a lower number of branches in the arista than does *willistoni*. However, the variation in all these traits is sufficient to make the measurements of the two species overlap broadly. Additional, and more satisfactory, distinguishing characters are given below.

Drosophila willistoni strains, the specific identity of which has been ascertained either by hybridization with known strains of the same species or by cytological methods, have been found in the following localities: Mexico, San Luis Potosí: Axtla; Guatemala: Quiriguá; Brazil, Territory Rio Branco: Rio Uraricoera, north of Boa Vista, Rio Mucajaí south of Boa Vista; Amazonas: several localities along Rio Negro between the mouth of Rio Branco and Manaos; Territory of Acre: Rio Môa, Cruzeiro do Sul, Japiim, Palmares; Territory of Guaporé: Porto Velho; Isle of Marajó: Cape Maguarí, Soure; Pará: Belem; Maranhão: Imperatriz, Carolina; Bahia: Salitre, Catuní; Goyaz: Palma, Monjolinho; Federal District: Rio de Janeiro; São Paulo: Pirassununga, Campinas, Mogi das Cruzes, São Paulo, Bertioga, Vila Atlantica, Itanhaem; Paraná: Paranaguá, Foz de Iguassu, Iguassu National Park; Rio Grande do Sul: Santo Angelo, Reuter; Bolivia: Santa Cruz de la Sierra; Argentina, Territory of Missiones, Iguassu.

Strains of *Drosophila paulistorum*, identified cytologically, have been collected in all the localities in Brazil and Bolivia in which *D. willistoni* has been found, except Catuni, and the places in the states of Paraná and Rio Grande do Sul; *D. paulistorum* has not been found in Mexico, Guatemala, or Argentina. The two species are, consequently, sympatric in a large territory including most of Brazil.

Drosophila equinoxialis *Dobzhansky*

A strain of flies from Tefé, Amazonas, which when collected was not distinguished from *willistoni*, proved to belong to a morphologically very similar but reproductively completely isolated species, described as *D. equinoxialis* Dobzhansky (1946). *D. equinoxialis* flies are similar to *D. willistoni*, although, as in the case of *D. paulistorum*, the variation curves overlap broadly. Professor H. T. Spieth discovered that the canal uniting the chitinous speramatheca with the vagina is cup-shaped in *willistoni* and vase-shaped in *equinoxialis* (Spieth, 1949).

Genetically or cytologically identified strains of *D. equinoxialis* have been collected in the following localities in Brazil. Territory of Rio Branco: Rio Uraricoera, north of Boa Vista, Rio Mucajaí; Amazonas: Tefé, several localities along the lower Rio Negro; Territory of Acre: Rio Môa, Japiim, Cruzeiro do Sul, Palmares; Territory of Guaporé: Porto Velho; Pará: Belem; Maranhão: Imperatriz, Carolina; Goyaz: Palma. The distribution area of *D. equinoxialis* is included in those of *D. willistoni* and *D. paulistorum*.

Drosophila tropicalis *Burla and da Cunha, species nova*

Male and female: Arista with 10–12 branches, 11 being the mean number. Antennae yellow, third segment darker, with a rather dense and long pilosity. Front dull yellow. Anterior orbitals slightly shorter than the posterior, middle one $\frac{2}{3}$ posterior. Two or three prominent orals. Face pale yellow. Carina short, gradually falling off below, not sulcate. Cheeks pale yellow, their greatest width about $\frac{1}{8}$ greatest diameter of eye. Eyes bright red with a short yellow pile.

Acrostichals in 6 rows, the lateral rows irregular. No prescutellars. Anterior scutellars parallel or slightly convergent. Thorax tannish-yellow, shining, pleurae lighter. Anterior sternopleural about $\frac{1}{2}$ posterior and much thinner, middle one slightly longer than the anterior. Legs pale yellow; apical bristles on first and second tibiae, preapicals on all three. Abdomen yellow with diffuse brown marginal bands not interrupted in the middle

and fading out laterally. Wings clear. Two prominent bristles at the apex of first costal section; third costal section with heavy bristles on its basal ½. Costal index ♀ 1.9–2.2, ♂ 1.8–2; 4th vein index ♀ 1.9–2.1, ♂ 1.8–1.95; 5 × index ♀ 1.4–2.0, ♂ 1.3–1.7.

Length of body ♀ 2.4–2.7, ♂ 2.00–2.25 mm.; wings 2.2–2.8 mm. Two anterior and two posterior Malpighian tubes, ends free.

Testes yellow with 2 outer and 3 inner coils. Spermathecae spherical, weakly chitinized, with an indentation.

Ventral receptacle a long tube forming a flat spiral bent into a W-shaped plate resting on the vagina.

Eggs—two filaments greatly expanded and flattened distally, about ⅗ as long as the egg itself.

Puparia—brownish yellow, horn very short, each anterior spiracle with 11–12 short branches.

Chromosomes—metaphase plate shows two pairs of V's, one of which is distinctly longer than the other, and a pair of rods.

Type in the Departamento de Zoologia of the Museum of São Paulo.

Remarks—The differences from *D. willistoni*, *D. paulistorum*, and *D. equinoxialis* are minor and overlapping, although doubtless significant statistically.

Geographic distribution — Brazil, Goyaz: Palma (type locality), Monjolinho; Territory of Rio Branco: Rio Uraricoera, north of Boa Vista, Rio Mucajaí; Amazonas: several localities along the lower Rio Negro; Territory of Acre: Rio Môa, Cruzeiro do Sul, Japiim, Palmares; Guaporé: Porto Velho; Island of Marajó: Cape Maguarí; Pará: Belem; Maranhão: Imperatriz, Carolina; Bolivia: Santa Cruz de la Sierra. *D. tropicalis* is, thus, sympatric with the other three sibling species.

Chromosomal Differences

The four sibling species have the same metaphasic chomosome groups: a pair of V-shaped X or Y-chromosomes, a pair of V-shaped second, and of rod-shaped third chromosomes. In the nuclei of the larval salivary gland cells, there are five chromosome strands that can be recognized by the patterns formed by the stainable discs which they contain (Plate 1); the strands designated as XR and XL correspond to the X-chromosome and carry the sex-linked genes; IIR and IIL are the two branches of the second chromosome and carry the second linkage group; and III is the chromosome which is rod-shaped at metaphase and carries the third linkage group. (The correspondence between cytologically visible chromosomes and linkage groups has been established by examination of certain chromosomal aberrations in *D. willistoni*, unpublished data).

The disc patterns in the free terminal portions of the XR, XL, IIR and IIL chromosomes are sufficiently similar in the four sibling species, so that these chromosomes can easily be recognized as such in all four species. The fifth chromosome strand, which must represent the third chromosome, is however strikingly and characteristically different (Plate 1). In *D. willistoni* the free end of the third chromosome contains three fairly dark discs, followed by a short light area and by a group of four very dark discs; at about the middle of the length of the portion drawn in Plate 1, there is a long section that contains only faint discs composed of dots, and which in most cells appears as a somewhat swollen "bulbous" segment. In *D. paulistorum* and *D. equinoxialis*, the free end of the third chromosome forms a spindle-shaped "head" with a fairly dark disc in the tip and two dark discs in the "neck"; this is followed proximally by a long segment with only light discs which is, however, not swollen; proximally to that is a segment in which some dark discs appear, and another light and often swollen section (Plate 1). In *D. tropicalis* the free end is light and usually expanded fan-like, followed by a group of four very dark discs, and by a light and often much swollen area (Plate 1). The free end of the third chromosome conclusively serves to identify *D. wil-*

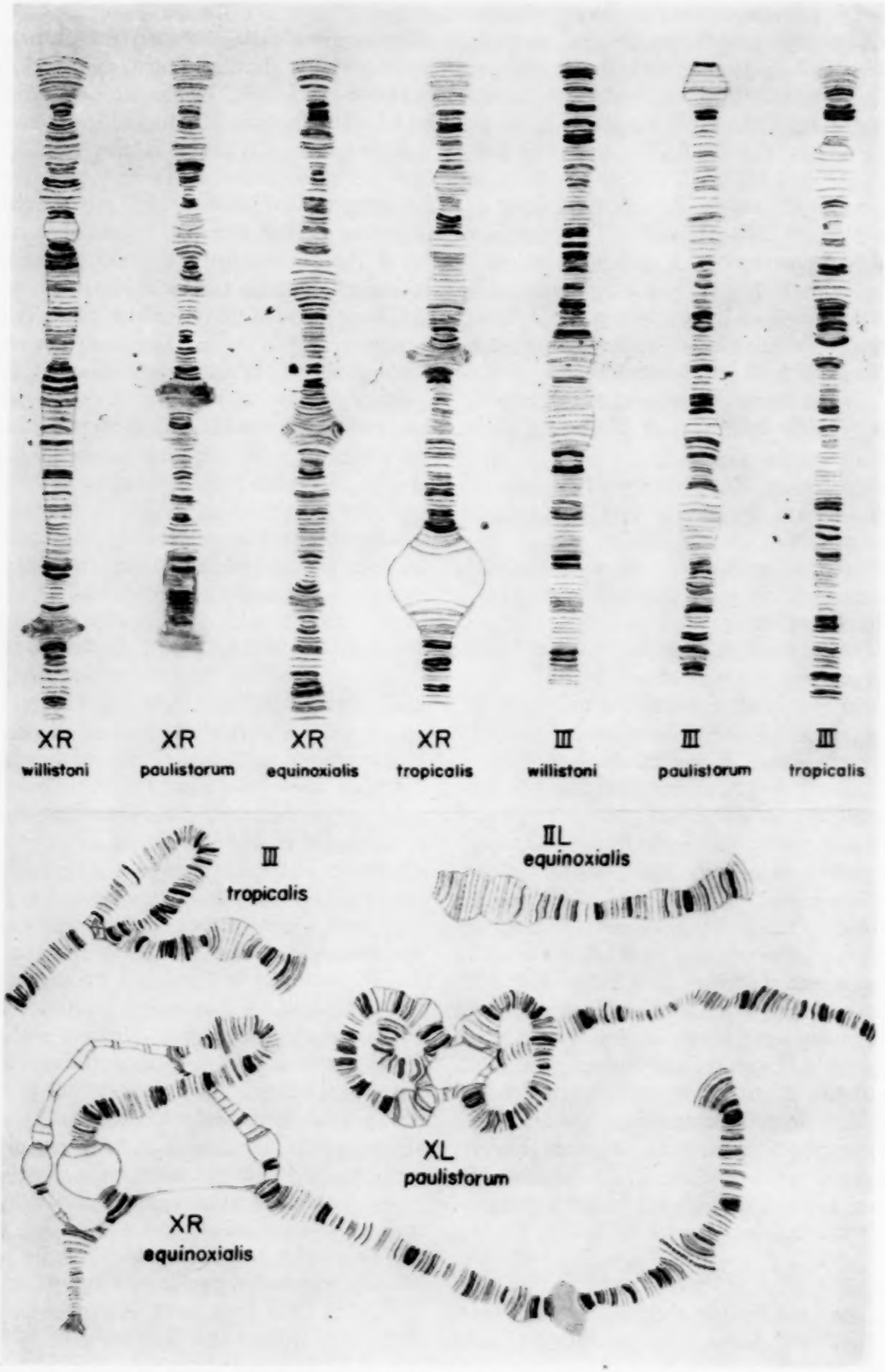

PLATE 1. The distal portions of the right limb of the X-chromosome, of the third chromosome, and some of the inversions found in natural populations of *Drosophila willistoni* and its relatives.

listoni and *D. tropicalis,* and to distinguish both of them from *D. paulistorum* and *D. equinoxialis.*

The terminal portions of the XR chromosome are similar in the four species but the middle and the basal parts, which contain characteristic mirror-image "repeat" areas (drawn in all four species in the upper portion of Plate 1) and large, light, usually strongly swollen "bulbs" (shown in XR of *tropicalis* in the upper, and XR of *equinoxialis* in the lower part of Plate 1), are different. The light bulbs are located at about the basal third of the length of XR in *D. tropicalis,* and within the basal fourth in the three other species. The "repeat" lies more proximally in *D. willistoni* than in *D. paulistorum* and in *D. equinoxialis,* and in the latter two slightly more proximally than in *D. tropicalis.* The XR chromosome can be used as well as the third chromosome for the identification of the species, except that *D. paulistorum* and *D equinoxialis* are similar.

The basal portions of the chromosome strands (attached to the chromocenter) are as characteristic for chromosomes and for species as are the terminal portions. The IIR and IIL strands have similar combinations of basal and terminal portions in *D. willistoni* and *D. tropicalis.* The same basal and terminal parts are recognizable also in *D. paulistorum* and *D. equinoxialis,* but in these two species the base of what in *D. willistoni* is designated as the IIR strand goes with the terminal portion of what in the latter species is the IIL strand, and vice versa. This situation shows that a pericentric inversion (including the centromere) has taken place in the phylogeny of the sibling species under consideration, so that the second chromosomes of *D. willistoni* and *D. tropicalis* differ from those of *D. paulistorum* and *D. equinoxialis* in the distribution of the genetic materials among the right and the left limbs.

The IIL strand of *D. equinoxialis* (Plate 1) differs from its homologues in the other three species in having a light and slightly swollen portion, somewhat resembling that in the third chromosome of *D. willistoni,* in a subterminal position.

The arrangement of the discs in the salivary gland chromosomes is known to reflect the linear arrangement of the genes. The phylogeny of the four species here described has, consequently, entailed a considerable amount of gene rearrangement, yet an amount not great enough to make the chromosomes unrecognizable by their disc patterns. The third chromosome has suffered more reconstructions in the phylogeny than did other chromosomes, as attested by the fact that the third chromosomes, except in *D. paulistorum* and *D. equinoxialis,* are identifiable only by a process of exclusion, since their disc patterns have no obvious similarities. Concentration of rearrangements in one of the chromosomes of a set is known to occur in natural populations of several species, such as *D. pseudoobscura* and *D. persimilis* (Dobzhansky, 1944) and *D. nebulosa* (Pavan, 1946), although the causes of this concentration are still obscure.

By the criterion of similarity of the disc patterns, *D. paulistorum* and *D. equinoxialis* are much closer to each other than they are to the other two species, or than these latter are among themselves. A reservation that must be made is that comparison of the disc patterns in chromosomes of species that can not be hybridized discloses only the major rearrangements that involve long sections of chromosomes, while changes in position of small groups of discs may be overlooked.

Morphological Differences between the Species

As far as the traits used in the formal description now standard for *Drosophila* species are concerned, *D. willistoni, D. paulistorum, D. equinoxialis,* and *D. tropicalis* show only slight, although statistically significant, differences. With the exception of the position of the anterior

scutellar bristles, which distinguishes *tropicalis* from the other three species, these differences are subject to so much variation and overlapping that determination of single specimens is often not reliable. We have therefore made a search for other differentiating traits, using flies from a series of cultures identified as to species by investigation of their chromosomes. Small differences indeed exist in almost every part of the body of the flies, and they give a characteristic "habi-

FIG. 1. Geographic distribution of *Drosophila willistoni* and its relatives. Localities in which the presence of *D. willistoni* has been ascertained by genetic or cytological tests are indicated by black circles, and the literature records of this species by open circles. The arrow points to the Isle of St. Vincent, the type locality of *D. willistoni*.

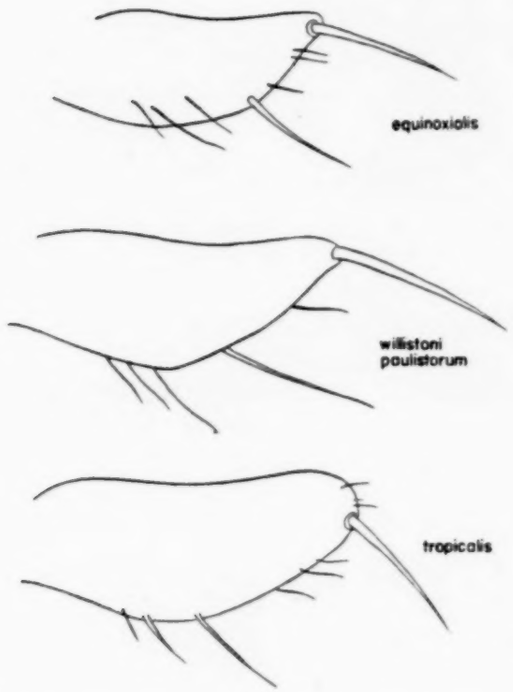

FIG. 2. Maxillar palpi of *Drosophila willistoni* and its relatives.

tus" to every species. Some of these differences prove clear enough to be used as traits for distinguishing the four species. Five traits are external and visible at magnifications of 20–50 times; these include the shape of the maxillar palpi, relative positions of the orbital bristles, relative width of the front, coloration of the ocelli, and shape of the apex of the vaginal plates. Three further traits demand dissection of the flies and preparation of microscopic slides.

D. tropicalis has the maxillar palpi inflated and broadly rounded at the apex, while the other three species have the palpi more slender and acuminate at the apex (fig. 2). The relative positions of the orbital bristles, shown in figure 3, permit one to distinguish *D. willistoni* from *D. paulistorum*. In *paulistorum* the base of the middle orbital lies only a little behind, and very close to the base of the first one. In *D. willistoni* the base of the middle orbital lies definitely between the anterior and the posterior ones. The distances between the bases of the orbital bristles have been measured in camera lucida drawings made from microscopic preparations. Taking the distance between the first and the third orbitals as 100, the distance between the first and the second varies between 8 and 22 (mean 15.7) in *paulistorum* and between 22 and 41 (mean 29.8) in *willistoni*. Figure 3 shows that the width of the front between the eyes is distinctly greater in *D. paulistorum* than in *D. willistoni*. The other two species, with respect to this and the preceeding traits, are intermediate between *paulistorum* and *willistoni*, these traits being useless for their identification. *D. equinoxialis* differs from the other species in having a lighter coloration of the ocelli, this difference not being subject to age changes.

The vaginal plates differ in shape in every species (fig. 4). In *D. tropicalis* they are broadly rounded at the apex; this

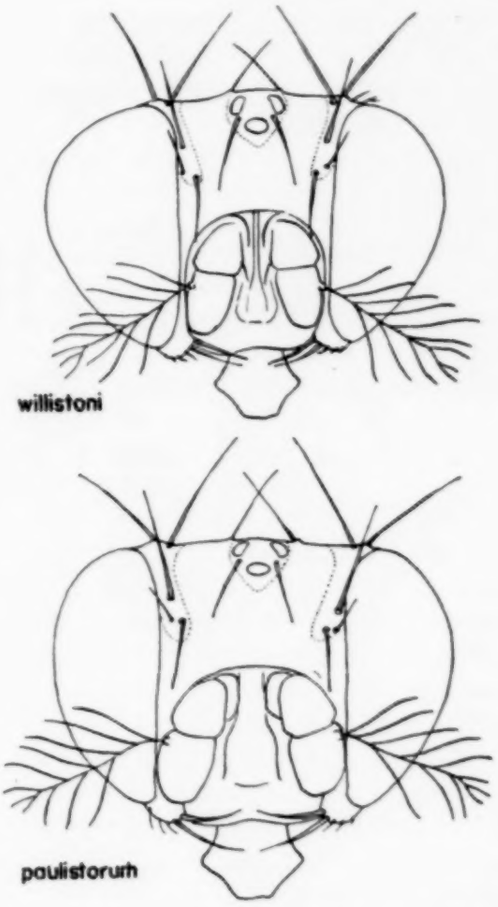

FIG. 3. Frontal view of the heads of *Drosophila willistoni* and *D. paulistorum*.

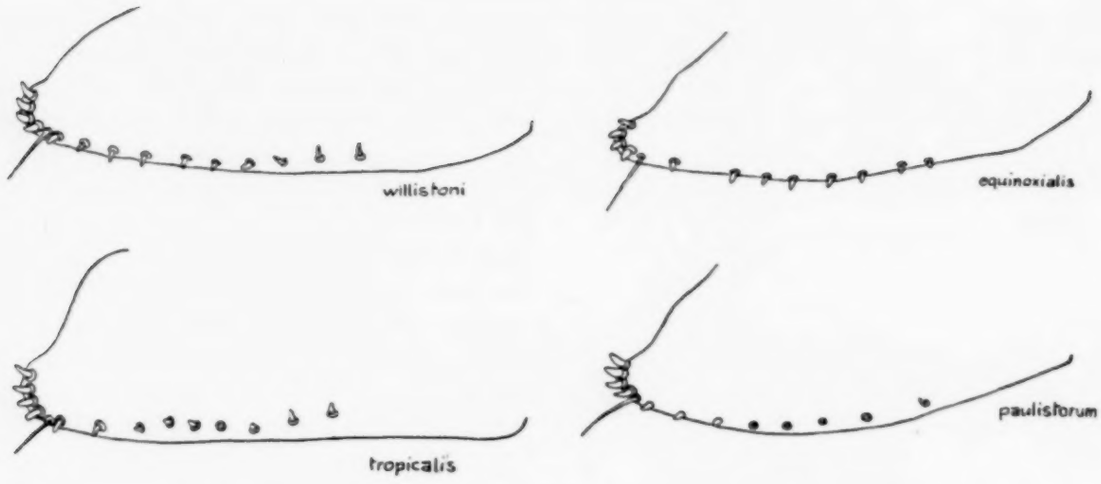

FIG. 4. Vaginal plates of *Drosophila willistoni* and its relatives.

trait, together with the shape of the palpi and the position of the anterior scutellar bristles, identifies this species conclusively. In *D. equinoxialis* the vaginal plates are acuminate at the apex. *D. willistoni* and *D. paulistorum* have vaginal plates intermediate in shape, making it rather difficult to distinguish these species from each other and from the preceeding two by this trait alone.

The chitinous spermathecae are more or less spherical in all species except in *D. tropicalis,* in which the width of the spermatheca is distinctly greater than its height (fig. 5). In *D. paulistorum* the spermatheca has folds that make the outlines of the organ uneven; in *D. willistoni* no external folds are present but the posterior part of the spermatheca is furrowed on the inside surface, and in *D. equinoxialis* neither folds nor furrows are noticeable. In *D. equinoxialis, D. paulistorum*

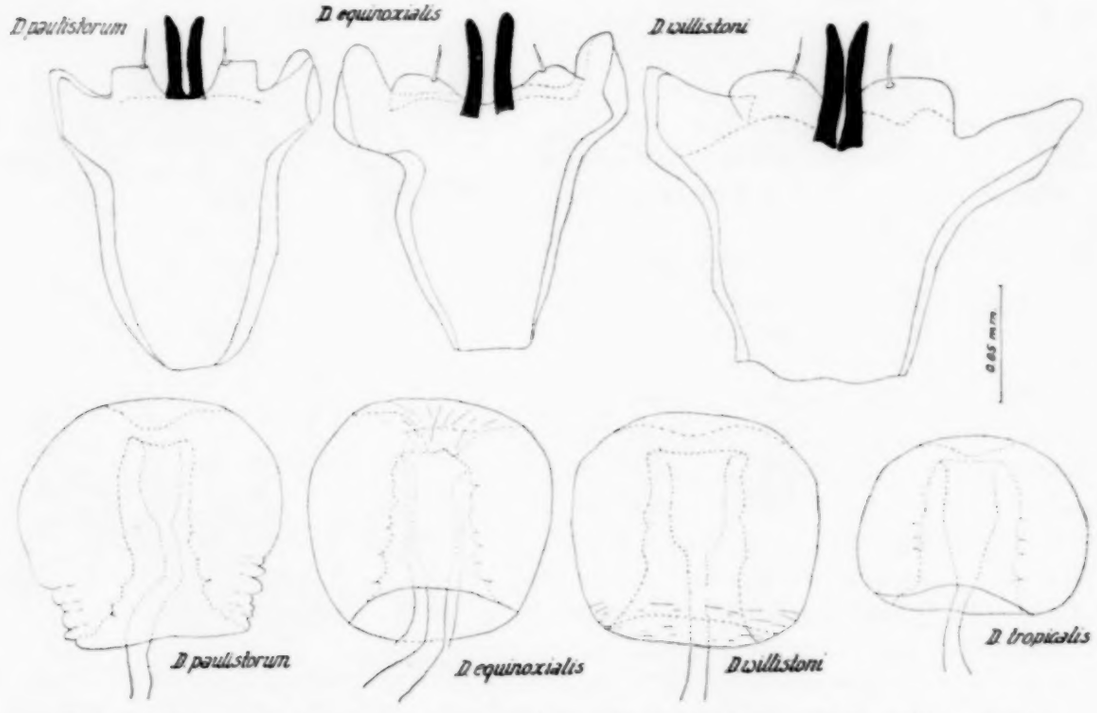

FIG. 5. Hypandria (above) and spermathecae (below) of *Drosophila willistoni* and its relatives.

and *D. tropicalis,* the surface of the sheath enclosing the spermathecal duct has tiny spines not noticeable in *D. willistoni* (fig. 5).

The hypandrium in male genitalia shows differences in the four species, especially in the shape of its posterior edge (directed upward in fig. 5) as may be noted in the figures. The hypandria of *D. paulistorum* and *D. tropicalis* seem to be alike in shape although the size is greater in the latter species. *D. willistoni* and *D. equinoxialis* also differ in the shape of the interior margin of the genital arch near the forceps (see Sales, 1947), which has a fairly large hook-shaped fold in the latter, and only a small tubercle in the former species. *D. paulistorum* is intermediate between the two species, and *D. tropicalis* is close to *D. willistoni* in this trait.

Reviewing the morphological differences between the four species under consideration, we find that species most different in some traits may be similar in other traits. *D. tropicalis* is on the whole the most distinctive species, and yet the shape of the internal process of the hypandrium in *D. tropicalis* and *D. paulistorum* is similar. *D. paulistorum* and *D. equinoxialis* are most similar in external morphology as well as in the disc patterns of the salivary gland chromosomes, and are distinguishable from each other principally by the color of the ocelli, by a slightly different shape of the vaginal plates and by the shapes of the spermatheca and of the hypandrium. *D. willistoni* is in many respects intermediate between *D. paulistorum* and *D. tropicalis,* and yet *D. willistoni* has the most distinctive hypandrium.

[*Note added in September 1949.* The above descriptions are based on examination of strains of the four sibling species coming from southern Brazil, from Goyaz, and from Acre. When, however, further strains, identified by inspection of their chromosomes, were examined from the equatorial part of Brazil (Rio Branco, Rio Negro, Pará), some of the traits, especially in *D. willistoni,* were found to be geographically variable. Thus, examination of a single female from each of 13 strains from Belem (Pará), 22 strains from Rio Branco, and 14 strains from Vila Atlantica (southern Brazil), all strains known to be *D. willistoni* gave the following results:

Scutellar Bristles	Belem	Rio Branco	Vila Atlantica
Divergent	23%	23%	86%
Parallel	62%	68%	14%
Convergent	15%	9%	0%

It is evident that this trait can not be relied upon to distinguish some strains of *D. willistoni* from *D. tropicalis.* These two species can still be discriminated by the shape of their palpi, but, unfortunately, this trait is not workable in dried material. *D. willistoni* from Vila Atlantica has a narrow front in 100% of the flies examined, but among the Belem flies only 69% have this condition. As many as 57% Vila Atlantica flies, and only 15% of the examined Belem flies, have 12 branches in at least one of their aristae. Comparison of cytologically identified *D. paulistorum* flies from Vila Atlantica and from Belem disclosed that divergent anterior scutellars are found in 70% of Vila Atlantica and 53% of Belem flies. The first and third orbitals are close to each other in 100% of Vila Atlantica and in only 40% of Belem flies.]

Physiological Differences

No systematic study of physiological properties of the four species has been made, but some differences between them were noted in the course of the work. If many single female cultures of *D. willistoni* and *D. paulistorum* are started simultaneously, the first cultures that produce grown-up larvae fit for dissection and study of salivary gland chromosomes are invariably *willistoni,* while among the last maturing cultures a large proportion are *paulistorum.* Thus, *willistoni* larvae,

despite their larger size, mature more rapidly then the smaller *paulistorum*. Cultures of *D. tropicalis* give uniformly excellent slides, the chromosomes being large, with clear disc patterns, and well spread. Conversely, *D. paulistorum,* and especially *D. equinoxialis,* give very inferior slides, with small, thin chromosomes, that seldom spread well. The nature of the physiological differences that lead to the different appearances of the chromosomes in preparations would be interesting to study from the standpoint of cyto- and chromosome chemistry.

Sexual Isolation and Lack of Hybrids

Dobzhansky (1946) found that when males of *D. willistoni* are placed together with females of *D. equinoxialis,* or vice versa, very few of the females are inseminated even after several weeks of exposure to males of the foreign species. Furthermore, the inseminated females fail to produce viable hybrid offspring. Spieth (1947) discovered that the courtship methods in the two species are different, *D. equinoxialis* males being more "lethargic" than *D. willistoni.* Thus the two species show a strong, though not absolute, sexual isolation, and the hybrid zygotes, if formed, are inviable. We have made similar experiments with all four species, using flies from cultures identified as to the species by cytological criteria.

Females and males to be used in the experiments were aged separately in vials with food for 4 to 6 days after their hatching from the pupae. Thereupon, 10 females of one and 10 males of another species were placed together in vials 25 × 95 mm. or 20 females and 20 males in vials 35 × 95 nim., left undisturbed for from 8 to 12 (mostly for 10) days, after which the females were dissected and their ventral receptacles as well as chitinous spermathecae examined for spermatozoa under a microscope. All experiments were made at room temperature (close to 25° C.). Since a single species of females and a single species of males were present in the vials, no "choice" of mates was available in these experiments. The results are summarized in table 2. The data for *willistoni* × *equinoxialis* crosses in this table are copied from Dobzhansky 1946.

Table 2. *Numbers of females dissected and percentages of them found inseminated in experiments in which no choice of mates was available*

Males	Females	Number dissected	Per cent inseminated
willistoni	*paulistorum*	69	5.7
willistoni	*equinoxialis*	545	1.5
willistoni	*tropicalis*	105	3.8
paulistorum	*willistoni*	230	51.3
paulistorum	*equinoxialis*	165	12.7
paulistorum	*tropicalis*	104	65.0
equinoxialis	*willistoni*	729	3.8
equinoxialis	*paulistorum*	94	0.0
equinoxialis	*tropicalis*	105	0.0
tropicalis	*willistoni*	112	0.0
tropicalis	*paulistorum*	115	27.8
tropicalis	*equinoxialis*	143	0.0

It can be seen that the four sibling species show varying degrees of sexual isolation from each other. Males of *equinoxialis* failed entirely to inseminate females of *paulistorum* and *tropicalis,* and inseminated only a few *willistoni* females. Similarily, *tropicalis* males failed to inseminate *willistoni* and *equinoxialis* females. *Willistoni* males inseminated small numbers of females of all three sibling species. In all these crosses sexual isolation is thus very strong or even complete. Quite different are the results in experiments in which *paulistorum* males are involved, for they inseminated from 12.7% (*equinoxialis*) to as many as 65% (*tropicalis*) females of other species. Females of *paulistorum* were not inseminated by *equinoxialis* males, rarely by *willistoni,* but frequently by *tropicalis* males. On the assumption that sexual isolation depends upon females repelling males of foreign species, made probable

by the observations of Streisinger (1948) and Bateman (1948), our results indicate that *paulistorum* males are either sexually more active than males of the other species, or that they are accepted without difficulty by females of all four species. This does not, however, account for the fact that females of *paulistorum* are inseminated rather readily by *tropicalis,* but not by *equinoxialis* or *willistoni* males. It seems necessary to assume that sexual isolation is less strong between *paulistorum* and *tropicalis* than between these and the other two species. It is possible that courtship or copulation techniques of *paulistorum* and *tropicalis* males are simliar in some essential respect that satisfies females of either species, but that these techniques differ in some respect that causes *paulistorum* males to be accepted and *tropicalis* males to be rejected by *willistoni* and *equinoxialis* females.

Small scale experiments were made in which males of one of the species were kept for 9–12 (mostly 10) days with females of their own and of a foreign species at room temperatures. The flies were 4–6 days old when placed together. A summary is presented in table 3, which also includes the data for *willistoni* × *equinoxialis* crosses taken from Dobzhansky (1946). The results obtained agree well enough with those found in the experiments in which no choice of mates was available. Homogamic matings (i.e., those between individuals of the same species) occur easily, and a majority of the conspecific females is found inseminated. Heterogamic matings (between individuals of different species) occur with difficulty, except that *tropicalis* males are accepted by *paulistorum* females.

Occurrence of heterogamic copulation and insemination does not guarantee that interspecific hybrids will be produced, since the sex cells of different species may have a lowered affinity or the hybrid zygotes may die at any stage of the life cycle. Some of the early experiments in which females and males of different species were together have produced progenies, but careful scrutiny showed that experimental errors were involved in these cases (these experiments are not included in tables 2 and 3). Otherwise, the interspecific matings, where they occur, produce no hybrids. Whether this is due to lack of fertilization or to inviability of the hybrids is unknown.

Absence of Gene Exchange between Species in Nature

Laboratory experiments have disclosed the existence of sexual isolation between the four sibling species; this isolation is incomplete in some instances, especially in the case of *D. paulistorum,* which copulates fairly readily with the other three. Females inseminated by males of foreign species fail, however, to produce hybrid progenies. Therefore, the reproductive isolation between the four species is complete, and they can coexist in the same territory without exchanging genes. Indeed, although the geographic distributions are far from perfectly known, it is certain that all four species are sympatric in an extensive territory (fig. 1). Within that territory they actually occur side by side, although the proportions of the four species in the population vary from one microenvironment to another, indicating that they have somewhat different ecological preferences. For example, in the five localities in the territories of Acre and Guaporé, population samples contained the following percentages of the four species (identified by cytological examination):

Locality	Strains examined	*willistoni*	*paulistorum*	*equinoxialis*	*tropicalis*
Cruzeiro do Sul	213	53	36	8	3
Rio Môa	60	33	18	3	45
Japiim	46	54	20	9	17
Porto Velho	53	32	49	13	6

D. tropicalis has been found most frequently in the interior of the "varzea" jungle along Rio Môa, and least fre-

TABLE 3. *Numbers of females dissected (n) and percentages of them found inseminated (%) in experiments in which a choice of mates was available*

Males	Females	Homogamic		Heterogamic	
		n	%	n	%
willistoni	*willistoni* + *paulistorum*	86	100	85	0
willistoni	*willistoni* + *equinoxialis*	71	65	73	0
paulistorum	*paulistorum* + *willistoni*	37	89	35	0
paulistorum	*paulistorum* + *equinoxialis*	10	100	9	11
equinoxialis	*equinoxialis* + *willistoni*	266	77	256	0.5
equinoxialis	*equinoxialis* + *paulistorum*	10	100	10	0
tropicalis	*tropicalis* + *willistoni*	105	100	112	0
tropicalis	*tropicalis* + *paulistorum*	45	100	42	50
tropicalis	*tropicalis* + *equinoxialis*	50	100	51	0

quently in "terra firme" forests of Palmares and Porto Velho. In the state of São Paulo, *D. paulistorum* is much commoner, relative to *D. willistoni*, on the very humid coast, and less common in the drier interior of the state, and much commoner during the warm season than during the cold.

Evidence, quite independent of laboratory experiments, is available to show that no gene exchange takes place in natural populations of the four species, despite their being sympatric to a large extent. Many of the individuals found in nature are heterozygous for inverted sections in their chromosomes. This phenomenom of structural heterozygosis will be dealt with in detail in another publication. What is important for us is that up to the present 42 different inversions have been discovered in populations of *D. willistoni*, that individuals that are not heterozygous for inversions are in the minority at most localities, and that inversions are found in all five chromosome limbs. In *D. paulistorum*, the frequency of inversions is considerably lower than in *D. willistoni*, and yet at least 20 different inversions have been recorded in all five chromosome limbs. Plate 1 shows the left limb of the X chromosome (XL) of *D. paulistorum* with two, apparently independent or tandem, inversions in heterozygous state. Most individuals of *D. equinoxialis* are inversion homozygotes, but one individual from Belem do Pará was heterozygous for an inversion in the basal portion of the right limb of the X chromosome (XR), shown in Plate 1. Another individual, from Cruzeiro do Sul, contained an inversion in the median part of the third chromosome. In *D. tropicalis* several individuals have been found in the Territory of Acre that had a subterminal inversion in the third chromosome shown in Plate 1. One individual from Porto Velho, Guaporé, was heterozygous for two inversions in the third chromosome, one identical with that pictured in Plate 1 and another in a more proximal position, apparently slightly overlapping the first. Finally, two individuals from Palmares, Acre, were heterozygous for a double inversion in the median part of the left limb of the second chromosome (IIL). Thus, 4 different inversions have been found in *D. tropicalis*.

The fundamental fact disclosed by the cytological studies on the four species under consideration is that each of the numerous inversions found in them is completely restricted to a single species. In other words, none of the inversions found in *D. willistoni*, for example, ever occurs in *D. paulistorum*, or vice versa. Now, if these species would intercross in nature so that a channel for effective gene exchange would be maintained between them, chromosomes or chromosome sections of one species would be found in populations of the other. This would be the case even if effective hybridization

were rare, for, unless foreign chromosome sections are rapidly eliminated by natural selection, they would accumulate in the populations. Let it be noted that while the absence of similar inversions in populations of sympatric species proves that effective hybridization between these species does not occur, their presence would not necessarily prove the opposite, because similar gene arrangements in chromosomes may be inherited by two or more species from their common ancestor. This is exactly what has been observed in the sibling species *D. pseudoobscura* and *D. persimilis* (Dobzhansky, 1944) and in *D. guaru* and *D. subbadia* (King, 1947).

Summary

The *willistoni* species group in tropical America contains four sibling species, *Drosophila willistoni* Sturtevant, *D. paulistorum* Dobzhansky and Pavan, *D. equinoxialis* Dobzhansky, and *D. tropicalis* Burla and da Cunha. In at least part of their area of distribution the four species occur together, sympatrically.

The four species are so much alike in their external morphological characters that they can be distinguished only with difficulty. Small differences are present in several traits that are generally used in Drosophila systematics, but the variability is great enough to make identification of species in single individuals hazardous. Several differences have been detected in traits not usually considered in describing Drosophila species which, after some practice, permit identification of individual flies, at least in fresh material.

The four species can always be recognized by the disk patterns in the chromosomes of larval salivary glands. The third chromosomes are very differently built in *willistoni*, *tropicalis*, and *paulistorum*, but similar in *paulistorum* and *equinoxialis*. The latter two species are in general most similar in chromosome structure, but can be differentiated by the structure of the left limb of the second chromosome. Speciation in the *willistoni* group has, consequently, involved major changes in the gene arrangement, without, however, altering beyond recognition the disc patterns in the chromosomes, except in the third.

The four species show varying degrees of sexual isolation from each other. *D. equinoxialis* and *D. willistoni* males seldom inseminate females of species other than their own. *D. tropicalis* males rather readily inseminate *D. paulistorum* females, and *D. paulistorum* males copulate fairly easily with females of the other three species. The degree of sexual isolation between any two species is proportional neither to morphological nor to chromosomal differences between them. Interspecific insemination does not result in production of hybrid progenies.

Numerous inversions have been found in natural populations of all species, especially *D. willistoni* and *D. paulistorum*. However, no inversion has ever been found in more than a single species. This proves that the reproductive isolation between these species is effective in nature.

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A NEW MEASURE OF SEXUAL ISOLATION

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INTRODUCTION

In recent years, a good deal of experimental work has been done on the detection and measurement of sexual isolation. One of the most common types of experiment, largely used for *Drosophila*, is to place a number of males of strain 1 with $n_{1,1}$ females of strain 1 (homogamic females) and $n_{1,2}$ females of strain 2 (heterogamic females). After a period of time the females are dissected, and $x_{1,1}$, the number of homogamic females inseminated, and $x_{1,2}$, the number of heterogamic females inseminated, are observed. The measure of isolation usually used is the *isolation index*, devised by Donald Charles and introduced by Stalker (1942). If we let $p_{1,1}=x_{1,1}/n_{1,1}$ and $p_{1,2}=x_{1,2}/n_{1,2}$ be the relative frequencies of insemination, then the isolation index is

$$b_{1,2}=\frac{p_{1,1}-p_{1,2}}{p_{1,1}+p_{1,2}}.$$

The isolation index ranges from $+1$ for complete isolation ($p_{1,2}=0$), through zero for no isolation ($p_{1,1}=p_{1,2}$), to -1 for complete negative isolation ($p_{1,1}=0$). There is also a reciprocal isolation index

$$b_{2,1}=\frac{p_{2,2}-p_{2,1}}{p_{2,2}+p_{2,1}},$$

obtained by placing strain 2 males with $n_{2,1}$ strain 1 (heterogamic) females and $n_{2,2}$ strain 2 (homogamic) females. Here $p_{2,2}$ and $p_{2,1}$ are the relative frequencies of homogamic and heterogamic matings respectively. In the notation employed in this paper the first subscript of a symbol refers to the strain of males involved and the second subscript refers to the strain of females. Thus, for homogamic matings the two subscripts are identical, while for heterogamic matings they are different. A slightly different convention is used for measures of isolation such as $b_{2,1}$, where the first subscript refers to the strain of males involved, and the second subscript refers to the heterogamic strain.

Charles also gave a test for the significance of an isolation index. Unfortunately his formula was printed ambiguously. In any event the ordinary Chi-square test for equality of two percentages gives the identical result and is easier to calculate. A further advance was made by Bateman (1949) when he introduced the concept of a *joint isolation index*, defined by him as the arithmetic mean of the two reciprocal simple isolation indexes; i.e.,

$$b_{1 \text{ and } 2}=\frac{b_{1,2}+b_{2,1}}{2}.$$

Bateman also introduced a measure of the "relative mating propensity" of the females, defined by

$$a_{1,2}=\frac{b_{1,2}-b_{2,1}}{2}.$$

DISCUSSION OF BATEMAN'S INDEXES

In this section and the next section we will suppose that very large samples are available, so that sampling fluctuations need not be considered. For simplicity, let us temporarily suppose that $p_{1,1}+p_{1,2}=1$ and $p_{2,2}+p_{2,1}=1$. Since approximately equal numbers of the two strains of females are ordinarily employed in each experiment, this implies that 50% of all females placed with a given strain of male are inseminated. The duration of contact is usually adjusted to make this as nearly true as possible. We then have $b_{1,2}=p_{1,1}-p_{1,2}$ and $b_{2,1}=p_{2,2}-p_{2,1}$. Then $b_{1 \text{ and } 2}=(b_{1,2}+b_{2,1})/2$

$=(p_{1,1}+p_{2,2}-p_{1,2}-p_{2,1})/2=(p_{1,1}+p_{2,2})/2-(p_{1,2}+p_{2,1})/2$; i.e., the joint isolation index becomes the average frequency of homogamic matings minus the average frequency of heterogamic matings. Hence, within the limitations of the type of experiment employed, the joint isolation index measures the effective degree of isolation of the two strains when in contact.

Similarly

$$a_{1,2}=(b_{1,2}-b_{2,1})/2$$
$$=(p_{1,1}-p_{1,2}-p_{2,2}+p_{2,1})/2$$
$$=(p_{1,1}+p_{2,1})/2-(p_{1,2}+p_{2,2})/2,$$

i.e., $a_{1,2}$ is the average frequency of insemination of strain 1 females minus the average frequency of insemination of strain 2 females. However, the biological interpretation of $a_{1,2}$ is not clear cut. On the one hand, $a_{1,2}$ may take a positive value simply because strain 1 females are sexually more receptive in general than strain 2 females; it is then a true measure of relative mating propensity. On the other hand, $a_{1,2}$ may take a positive value because strain 1 males have developed some obnoxious characteristic, and by natural selection, strain 1 females have "become used to this characteristic" and no longer "mind it." Hence, the frequency of matings of strain 1 males with strain 2 females is lowered, while the other three types of matings are not affected. Such a situation seems to exist with respect to the yellow mutant in *D. subobscura* (Rendel, 1945) and *D. pseudoobscura* (Tan, 1946). We may call this situation a one-way sexual preference after Dobzhansky and Streisinger (1944). In either of the two above situations the net result is more inseminations among strain 1 females than among the strain 2 females, and so we suggest that $a_{1,2}$ be called the *excess insemination index* of strain 1 over strain 2.

Disadvantages of the Present Indexes

It is well known that the value of the Charles-Stalker isolation index depends on the length of time the flies are left together. As this time increases, both $p_{1,1}$ and $p_{1,2}$ approach one, and hence $b_{1,2}$ approaches zero, if heterogamic matings take place at all. It is for this reason that so much pains are taken to have $p_{1,1}+p_{1,2}=1$. When $p_{1,1}+p_{1,2}$ is large, $b_{1,2}$ will usually be close to zero, and its value gives little information about the possible existence of isolation. On the other hand, as long as $p_{1,1}+p_{1,2}$ does not much exceed one, $b_{1,2}$ will equal zero if and only if there is random mating (no isolation). However, even under these conditions, $b_{1,2}=0$ is the only fixed point on the isolation index scale. Luckily, this is by far the most important point. We do want to know whether or not there is isolation (i.e. whether or not $b_{1,2}=0$). On the other hand, if isolation has been found, the precise value of $b_{1,2}$ is of less importance. For example, it makes relatively little difference whether $b_{1,2}$ equals .20 or .25, say. However, it would still be desirable to have a measure that would be less sensitive to the duration of the experiment.

This disadvantage becomes more serious when we come to the joint isolation index. This index is zero only if $b_{1,2}+b_{2,1}=0$, or $b_{1,2}=-b_{2,1}$. Even when considerable care is taken, the over-all frequency of insemination may be different in two reciprocal experiments. Hence the reciprocal isolation indexes, $b_{1,2}$ and $b_{2,1}$, will be measured by different scales, so that where they should be equal but of opposite sign, they will be unequal with a spurious non zero joint isolation index resulting. Conversely the joint isolation index may become zero when joint isolation exists.

Another defect in the present theory of the joint isolation index is that no test of significance has been published.

A New Measure of Isolation

The ideal way to introduce any sort of quantitative measure is as follows. One first specifies the biological situation. Next a mathematical model is con-

structed which gives the salient aspects of the biological situation in abstract form. This model will always be an oversimplification of the true situation, and it is the task of the biometrician to make the model as realistic as possible without its being too unwieldy. The mathematical model will then dictate the essential nature of the quantity to be measured, and the measure to be used. The development of efficient methods of estimation, and of tests of significance, is then a purely technical problem.

We now set up the following model. Strain 1 males are placed with $n_{1,1}$ strain 1 females and $n_{1,2}$ strain 2 females. Suppose there is a fixed probability of insemination each time a male meets a virgin strain 1 female, and in any small unit of time there is a fixed probability that any virgin female will be met by a male. According to Levene and Dobzhansky (1945) this assumption seems reasonable. There will then be a fixed probability, say $c_{1,1}dt$, that any particular virgin female will be inseminated during the interval t to $t+dt$. We further suppose, that the probability that any virgin female is inseminated during this time interval is independent of this probability for any other female. This assumption is not quite valid, since, if any female is being inseminated, fewer males are available to meet the other females. However, this should cause no serious difficulty if the duration of the experiment is long compared with the duration of a single copulation.

With these assumptions the probability that any particular strain 1 female will be inseminated in an experiment of duration t, will be

$$p_{1,1}=1-e^{-c_{1,1}t_1}. \qquad (1)$$

This last equation resembles that for a monomolecular reaction. Similarly the probability that a strain 2 female will be inseminated is

$$p_{1,2}=1-e^{-c_{1,2}t_1}.$$

Then a reasonable measure of isolation is the ratio of the two elementary probabilities of insemination,

$$h_{1,2}=\frac{c_{1,2}}{c_{1,1}}. \qquad (2)$$

From equation (1) we have

$$e^{-c_{1,1}t_1} = 1 - p_{1,1}=q_{1,1}$$

or

$$c_{1,1}t_1 = -\ln q_{1,1},$$

where $q_{1,1}$ is the relative frequency of *not* inseminated strain 1 females, and $\ln q_{1,1}$ is the natural logarithm of $q_{1,1}$ or 2.30259 times the common logarithm of $q_{1,1}$. Similarly

$$c_{1,2}t_1=-\ln q_{1,2},$$

where the meaning of $q_{1,2}$ is obvious. Then

$$h_{1,2}=\frac{c_{1,2}}{c_{1,1}}=\frac{c_{1,2}t_1}{c_{1,1}t_1}=\frac{-\ln q_{1,2}}{-\ln q_{1,1}}. \qquad (3)$$

Evidently $h_{1,2}$ is independent of the duration t_1, of the experiment.

Now $h_{1,2}$ takes the values zero for complete isolation, one for no isolation, and infinity for complete reverse isolation. It is more convenient to have a measure which varies from -1 to $+1$, as does the isolation index. Such a measure is

$$K_{1,2}=\frac{1-h_{1,2}}{1+h_{1,2}}=\frac{\log q_{1,1}-\log q_{1,2}}{\log q_{1,1}+\log q_{1,2}},$$

which we will call the *coefficient of isolation*. Either natural or common logarithms may be used in computing $K_{1,2}$. The coefficient of isolation is $+1$ for complete isolation, zero for no isolation, and -1 for complete reverse isolation.

Tables 1, 2, and 3 show the comparative behavior of the isolation index and the coefficient of isolation for certain illustrative values of $p_{1,1}$ and $p_{1,2}$.

There is one difference in behavior between the Charles-Stalker isolation index and our coefficient of isolation. The isolation index is $+1$ only when $p_{1,2}=0$ (or $q_{1,2}=1$). This is as it should be, since only then is there complete biological isolation. On the other hand the coefficient of isolation is $+1$ if either $p_{1,2}=0$ or $p_{1,1}=1$. However, this is not

very serious, since according to formula 1, the probability $p_{1,1}$ can equal one only if the time, t_1, is infinite.

The coefficient of isolation $K_{1,2}$ and the isolation index $b_{1,2}$ always have the same sign. In general $K_{1,2}$ is numerically larger than $b_{1,2}$, but there is no fixed relationship between the two, since $b_{1,2}$ is affected by the duration of the experiment while $K_{1,2}$ ideally is not. Actually our model is not quite accurate, and $K_{1,2}$ is affected by the duration, but to a smaller extent than $b_{1,2}$.

TABLE 1. *Values of isolation index $b_{1,2}$ and coefficient of isolation $K_{1,2}$ when 10% of all females are inseminated*

% strain 1 inseminated $100p_{1,1}$	% strain 2 inseminated $100p_{1,2}$	$b_{1,2}$	$K_{1,2}$
10	10	0	0
12	8	.20	.210
15	5	.50	.520
19	1	.90	.908
19.9	0.1	.99	.992

TABLE 2. *Values of isolation index $b_{1,2}$ and coefficient of isolation $K_{1,2}$ when 50% of all females are inseminated*

% strain 1 inseminated $100p_{1,1}$	% strain 2 inseminated $100p_{1,2}$	$b_{1,2}$	$K_{1,2}$
50	50	0	0
51	49	.02	.0289
60	40	.20	.285
70	30	.40	.478
80	20	.60	.756
90	10	.80	.913
99	1	.98	.994
100	0	1	1

TABLE 3. *Values of isolation index $b_{1,2}$ and coefficient of isolation $K_{1,2}$ when 90% of all females are inseminated*

% strain 1 inseminated $100p_{1,1}$	% strain 2 inseminated $100p_{1,2}$	$b_{1,2}$	$K_{1,2}$
90	90	0	0
92	88	.022	.087
95	85	.056	.225
98	82	.089	.391
99	81	.100	.470
99.9	80.1	.110	.621
as $p_{1,1}\to 1$	$p_{1,2}=.80$	$b_{1,2}\to 1/9$	$K_{1,2}\to 1$

The coefficient of isolation for the reciprocal experiment using strain 2 males is defined in the same manner as

$$K_{2,1}=\frac{\log q_{2,2}-\log q_{2,1}}{\log q_{2,2}+\log q_{2,1}}. \qquad (4)$$

The *coefficient of joint isolation* can then be defined as

$$K_{1 \text{ and } 2}=(K_{1,2}+K_{2,1})/2, \qquad (5)$$

and the excess of strain 1 inseminations over strain 2 inseminations can be measured by the *coefficient of excess insemination* of strain 1 over strain 2

$$m_{1,2}=(K_{1,2}-K_{2,1})/2. \qquad (6)$$

The coefficient of joint isolation measures the true reproductive isolation between the two strains under the (artificial) conditions of the experiment, while the coefficient of excess insemination can serve as a measure of the extent to which the gene flow between the two strains is in one direction only.

SAMPLING THEORY

Up to now we have assumed our samples were so large that no question of sampling error arose. We must now consider sampling problems. The symbols $q_{1,1}$, $K_{1,2}$, etc. will now refer to sample values, and we will add a tilde, as $\tilde{K}_{1,2}$ etc. to denote the true population values. The estimate of $\tilde{K}_{1,2}$ from a homogeneous sample is

$$K_{1,2}=\frac{\log q_{1,1}-\log q_{1,2}}{\log q_{1,1}+\log q_{1,2}}=\frac{(\log y_{1,1}-\log n_{1,1})-(\log y_{1,2}-\log n_{1,2})}{(\log y_{1,1}-\log n_{1,1})+(\log y_{1,2}-\log n_{1,2})}, \qquad (7)$$

where $y_{1,1}$ is the number of strain 1 females *not* inseminated, i.e., $y_{1,1}=n_{1,1}-x_{1,1}$, etc.

Similarly the coefficient of isolation when strain 2 males are used is

$$K_{2,1}=\frac{\log q_{2,2}-\log q_{2,1}}{\log q_{2,2}+\log q_{2,1}}=\frac{(\log y_{2,2}-\log n_{2,2})-(\log y_{2,1}-\log n_{2,1})}{(\log y_{2,2}-\log n_{2,2})+(\log y_{2,1}-\log n_{2,1})}. \quad (8)$$

In both these formulas either natural or common logarithms may be used.

The sample value of the coefficient of joint isolation is

$$K_{1 \text{ and } 2}=(K_{1,2}+K_{2,1})/2, \quad (9)$$

while the sample value of the coefficient of excess insemination of strain 1 over strain 2 is

$$m_{1,2}=(K_{1,2}-K_{2,1})/2. \quad (10)$$

As is the case with most statistics based on frequency data, exact tests of significance for coefficients of isolation are too cumbersome to be useful. However, in large samples these measures are nearly normally distributed, so that tests of significance can be carried out if we know the standard errors. The exact standard errors would be too difficult to obtain and to compute, but, since their use is only valid for large samples, large sample approximations (obtained by the "delta method") will do.

The approximate standard errors of the coefficients of isolation are

$$\sigma_{K_{1,2}}=\sqrt{\frac{(1+K_{1,2})^2}{4(\ln q_{1,1})^2}\left[(1-K_{1,2})^2\frac{p_{1,1}}{n_{1,1}q_{1,1}}+(1+K_{1,2})^2\frac{p_{1,2}}{n_{1,2}q_{1,2}}\right]} \quad (11)$$

$$\sigma_{K_{2,1}}=\sqrt{\frac{(1+K_{2,1})^2}{4(\ln q_{2,2})^2}\left[(1-K_{2,1})^2\frac{p_{2,2}}{n_{2,2}q_{2,2}}+(1+K_{2,1})^2\frac{p_{2,1}}{n_{2,1}q_{2,1}}\right]}. \quad (12)$$

Natural logarithms must be used here. The approximate standard error of the coefficient of joint isolation and the coefficient of excess insemination is

$$\sigma_{K_{1 \text{ and } 2}}=\sigma_{m_{1,2}}=\sqrt{(\sigma^2{}_{K_{1,2}}+\sigma^2{}_{K_{2,1}})/4}. \quad (13)$$

It should be noted that the true standard errors involve the true values of the p's etc. However, provided the samples are large and neither of the p's is close to zero or one, we may drop the tildes throughout, as has been done above, and use the estimated standard errors for our tests. We have pointed out above that the true $\tilde{p}$'s can never equal one; however, in finite samples it may happen that all the females of one strain are inseminated. In such a case a rough value of K may be obtained by supposing half a female was not inseminated, but no standard error should be attached to such an estimate.

The author has obtained tests that are somewhat more accurate and efficient than the tests using the estimated standard error, but they are very laborious to compute and will not be published here. The tests above will be satisfactory for most purposes, with one exception. For testing whether a *simple* coefficient (not a joint coefficient) of isolation such as $K_{1,2}$ equals zero, i.e., to test whether isolation exists, the ordinary χ^2 test is easily computed and is more reliable.

A confidence interval within which we may be reasonably sure the true value of one of these coefficients lies, may be obtained by taking the sample value plus and minus a suitable multiple of its estimated standard error. Finally, if two experiments under different conditions give values $K_{1,2}$ and $K'_{1,2}$ for the coefficient of isolation, we can test for equality of the true coefficients by comparing the difference of $K_{1,2}$ and $K'_{1,2}$ with its standard error, using the usual formula for the standard error of the difference of two independent quantities,

$$\sigma_{(K_{1,2}-K'_{1,2})}=\sqrt{\sigma^2{}_{K_{1,2}}+\sigma^2{}_{K'_{1,2}}}. \quad (14)$$

This test is much easier to apply than

Bartlett's test suggested by Snedecor (1945; 1946, page 203.) Furthermore, Bartlett's test is for the existence of a "second order interaction" and is not precisely equivalent to a test of equality of coefficients of isolation. In addition, this test can be extended to joint coefficients in an obvious way. The author has devised a test for the equality of three or more coefficients of isolation, but it is very laborious to use and is beyond the scope of the present paper.

An Example

We close with a numerical example, taken from Dobzhansky and Streisinger (1944). Letting the strain of *Drosophila prosaltans* from Huichihuayan, Mexico, be strain 1, and the strain from Guatemala City, Guatemala, be strain 2, Dobzhansky and Streisinger found $n_{1,1}=92$, $p_{1,1}=.717$, $n_{1,2}=92$, $p_{1,2}=.380$, $n_{2,2}=79$, $p_{2,2}=.367$, $n_{2,1}=80$, $p_{2,1}=.487$. They give the isolation indexes $b_{1,2}=.31$, $b_{2,1}=-.14$. Bateman gives the joint isolation index $b_{1 \text{ and } 2}=.09$ and his "mating preference index" $a_{1,2}=.23$. We find the coefficients of isolation

$$K_{1,2}=\frac{\log(.283)-\log(.620)}{\log(.283)+\log(.620)}$$

$$=\frac{-1.2623+.4780}{-1.2623-.4780}=.450,$$

using natural logarithms, and $K_{2,1}=-.187$. As stated above, the coefficients of isolation are numerically larger than the corresponding indexes. The coefficient of joint isolation is $K_{1 \text{ and } 2}=.132$, and the coefficient of excess insemination of strain 1 over strain 2 is $m_{1,2}=.318$.

The standard errors are

$$\sigma_{K_{1,2}}=\sqrt{\frac{(1.4501)^2}{4(-1.2623)^2}\left[(.5499)^2\left(\frac{.717}{92(.283)}\right)+(1.4501)^2\left(\frac{.380}{92(.620)}\right)\right]}$$

$$=\sqrt{.007962}=.089,$$

$$\sigma_{K_{2,1}}=\sqrt{.01439}=.120,$$

$$\sigma_{K_{1 \text{ and } 2}}=\sigma_{m_{1,2}}=\sqrt{(.007962+.01439)/4}=.0747.$$

Writing our coefficients as $K_{1,2}=.45\pm.09$, $K_{2,1}=-.19\pm.12$, $K_{1 \text{ and } 2}=.13\pm.07$, and $m_{1,2}=.32\pm.07$, we see that the coefficient of isolation using Huichihuayan males is significant, while that using Guatemala males is not. This agrees with the more accurate Chi-square test used by Dobzhansky and Streisinger ($\chi^2=21.6$ and 2.6 respectively). We see that $m_{1,2}$ is significant, while $K_{1 \text{ and } 2}$ is not quite significant ($t=1.76$). The standard errors can also be used for giving confidence intervals; for example, if we state that the true value lies on the interval given by the observed value plus or minus twice the standard error, in the long run approximately 95% of such statements will be true. Here we can say, with this degree of confidence, that $.27\leq\tilde{K}_{1,2}\leq.63$, $-.43\leq\tilde{K}_{2,1}\leq.05$, $-.01\leq\tilde{K}_{1 \text{ and } 2}\leq.27$ and $.18\leq\tilde{m}_{1,2}\leq.46$. If we added and subtracted three times the standard error, approximately 99.7% of such statements would be true, etc.

Summary

An improved measure of sexual isolation, called the *coefficient of isolation*, is introduced for experiments where strain 1 males are placed with strain 1 and strain 2 females and the number of intra-strain and inter-strain inseminations are counted. The new measure is less affected by changes in the length of time the organisms are together than is the isolation index. This advantage is particularly important when a joint measure of isolation is calculated from an experiment using strain 1 males and another experiment using strain 2 males. Standard errors are given for both simple and joint coefficients. Among other things

this furnishes an improved and simpler test for equality of isolation in two different experiments. As an example, computations are made for strains of *Drosophila prosaltans* from Huichihuayan and Guatemala (Dobzhansky and Streisinger, 1944). The coefficient of joint isolation is not significant.

Appendix: Definitions and Formulas

$n_{1,1}$ = number of strain 1 ♀'s placed with strain 1 ♂'s.

$n_{1,2}$ = number of strain 2 ♀'s placed with strain 1 ♂'s.

$n_{2,1}$ = number of strain 1 ♀'s placed with strain 2 ♂'s.

$n_{2,2}$ = number of strain 2 ♀'s placed with strain 2 ♂'s.

$y_{1,1}$ = number of strain 1 ♀'s not inseminated when with strain 1 ♂'s.

$q_{1,1} = y_{1,1}/n_{1,1}$.

$y_{1,2}$, $y_{2,1}$, $y_{2,2}$, $q_{1,2}$, $q_{2,1}$, $q_{2,2}$ similarly defined.

$K_{1,2}$ = coefficient of isolation when strain 1 ♂'s are placed with strain 1 ♀'s and strain 2 ♀'s.

$K_{2,1}$ = coefficient of isolation using strain 2 ♂'s.

$K_{1 \text{ and } 2}$ = coefficient of joint isolation of strains 1 and 2.

$m_{1,2}$ = coefficient of excess insemination of strain 1 over strain 2.

$$K_{1,2} = \frac{\log q_{1,1} - \log q_{1,2}}{\log q_{1,1} + \log q_{1,2}} = \frac{(\log y_{1,1} - \log n_{1,1}) - (\log y_{1,2} - \log n_{1,2})}{(\log y_{1,1} - \log n_{1,1}) + (\log y_{1,2} - \log n_{1,2})}.$$

$$K_{2,1} = \frac{\log q_{2,2} - \log q_{2,1}}{\log q_{2,2} + \log q_{2,1}} = \frac{(\log y_{2,2} - \log n_{2,2}) - (\log y_{2,1} - \log n_{2,1})}{(\log y_{2,2} - \log n_{2,2}) + (\log y_{2,1} - \log n_{2,1})}.$$

$K_{1 \text{ and } 2} = (K_{1,2} + K_{2,1})/2.$

$m_{1,2} = (K_{1,2} - K_{2,1})/2.$

$$\sigma_{K_{1,2}} = \sqrt{\frac{(1+K_{1,2})^2}{4(\ln q_{1,1})^2}\left[(1-K_{1,2})^2\frac{p_{1,1}}{n_{1,1}q_{1,1}} + (1+K_{1,2})^2\frac{p_{1,2}}{n_{1,2}q_{1,2}}\right]}$$

$$\sigma_{K_{2,1}} = \sqrt{\frac{(1+K_{2,1})^2}{4(\ln q_{2,2})^2}\left[(1-K_{2,1})^2\frac{p_{2,2}}{n_{2,2}q_{2,2}} + (1+K_{2,1})^2\frac{p_{2,1}}{n_{2,1}q_{2,1}}\right]}$$

$$\sigma_{K_{1 \text{ and } 2}} = \sigma_{m_{1,2}} = \sqrt{(\sigma^2_{K_{1,2}} + \sigma^2_{K_{2,1}})/4}.$$

Test for equality of two independent coefficients of isolation, $K_{1,2}$ and $K'_{1,2}$: Compare $K_{1,2} - K'_{1,2}$ with its standard error, $\sigma_{K_{1,2}-K'_{1,2}} = \sqrt{\sigma^2_{K_{1,2}} + \sigma^2_{K'_{1,2}}}$.

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SEASONAL VARIATION IN GENE ARRANGEMENT FREQUENCIES OVER A THREE-YEAR PERIOD IN *DROSOPHILA ROBUSTA* STURTEVANT

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INTRODUCTION

Previous studies of the gene arrangements of *Drosophila robusta* have dealt with their broad geographical distribution in the eastern United States (Carson and Stalker, 1947) and their distribution over an 18-mile altitudinal transect in the mountains of Tennessee (Stalker and Carson, 1948). In both instances, geographical gradients, or clines, in the frequencies of many of the chromosomal types were found. Over the broad geographical range of the species, these clines are gradual, and in a number of cases show distinct north-south relationships; on the mountainside, some, at least, are very steep.

Whereas the preceding studies have dealt with the distribution of the gene arrangements in space, the present paper deals largely with their distribution in time. The data presented herein were obtained from an intensive study of the frequencies of the various gene arrangements in a single local population near St. Louis, Missouri, over a three-year period.

MATERIALS AND METHODS

The specimens on which the present studies are based were collected from traps set in a portion of an approximately 25-acre woods located just east of the Stacey Park Reservoir near Olivette, St. Louis County, Missouri. The trapping area within this woods consisted of a sector (approximately 50 × 175 yards) of a valley through which a small intermittent stream runs. The larger trees bordering this stream are mostly elm, hickory and oak, although the latter are largely confined to the drier slopes above the stream where little or no trapping was done. Approximately 40 traps were used in making each collection; these were suspended on string from the branches of shrubs and small trees, anywhere from 10 to 25 feet apart. Insofar as possible, the traps were hung in the same positions from year to year. Ripe banana mash was used almost exclusively for bait. This general method, involving the use of a large number of small traps, has been found to be more satisfactory than the use of a small number of large traps.

Regular collections were made during the years 1946, 1947, and 1948. In 1946, collections were made more or less continuously from February through December; in 1947 and 1948, collections were made in spring and fall. In September of 1946, an additional collection was made from another woods ("North-South Woods") in University City, Missouri, three miles east of the main collecting locality in Olivette.

After collection, the flies were brought immediately to the laboratory and each wild-caught female was placed in a separate culture vial. If the wild female had been inseminated in nature, the usual procedure for making chromosome arrangement analyses consisted of examination of a salivary gland chromosome smear of a single F_1 female larva. For any given chromosome arm, this method permits the detection of two "wild" chromosome arrangements, one contributed by each wild parent. Such a sample has been conveniently designated as an "egg sample" by Dobzhansky and Levene (1948). In terms of natural populations, egg samples represent the chromosomal constitution of fertilized eggs which normally would have been laid in nature by the wild females. As the F_1 larvae are raised un-

TABLE 1A. *Frequencies (in per cent) of the gene arrangements in the left and right arms of chromosome X of* Drosophila robusta *for the years 1946, 1947 and 1948 at Olivette, Missouri*

Period	n	Left arm Gene arrangement			Right arm Gene arrangement		
		XL	XL-1	XL-2	XR	XR-1	XR-2
1946							
I. Mar. 5–Apr. 6	106	99.1	0.9	0.0	44.3	55.7	0.0
II. Apr. 13–May 15	188	98.0	1.0	1.0	43.1	55.8	1.1
III. May 18–Jun. 1	344	98.8	0.9	0.3	44.2	54.9	0.9
IV. Jun. 17–19	459	98.7	0.4	0.9	42.5	56.2	1.3
V. July 3–9	379	97.4	1.6	1.0	42.5	55.7	1.8
VI. July 23–Aug. 6	343	97.7	1.4	0.9	39.6	59.2	1.2
VII. Aug. 15–Sep. 3	297	98.3	1.4	0.3	41.1	57.2	1.7
VIII. Sep. 13–24	311	99.0	1.0	0.0	38.6	59.8	1.6
IX. Oct. 14–Dec. 10	160	98.8	0.6	0.6	43.8	54.4	1.8
1947							
X. May 19–Jun. 7	320	96.8	1.6	1.6	44.4	51.5	4.1
XI. Sep. 28–Oct. 17	302	97.7	1.6	0.7	47.0	50.0	3.0
1948							
XII. Jun. 5–14	480	95.8	2.7	1.5	45.4	51.5	3.1
XIII. Sep. 30–Oct. 9	173	97.7	0.6	1.7	45.7	49.7	4.6
Total I–XIII	3862	97.8	1.3	0.9	43.1	54.8	2.1

der optimal conditions in the laboratory, a given egg sample is presumably a random one. In cases where the wild-caught female proved to be virgin, she was mated to a wild male captured on or about the same day. Smears of single F_1 female larvae were also made from such crosses; these data have been used as egg samples, although they differ in that the mating was made in the laboratory rather than under natural conditions.

The chromosomal constitution of some wild males was analyzed by crossing them to virgin laboratory females of known constitution. In most of these cases, the salivary gland chromosomes of seven F_1 larvae were smeared. Examination of these smears permits one to state with a high degree of accuracy what arrangements were actually present in the wild male. Such a sample has been designated an "adult male sample" by Dobzhansky and Levene (1948). Further details of these methods for obtaining quantitative data on frequencies of gene arrangements may be found in Carson and Stalker (1947). The data presented in this paper are based on approximately 22,000 chromosome arm examinations.

RESULTS

1. Seasonal and year-to-year variation in gene arrangement frequencies at Olivette, Missouri

Table 1A shows the frequencies of the three arrangements in the left arm (XL, XL–1, and XL–2) and the three in the right arm (XR, XR–1, and XR–2) for the three years. The 1946 data have been

TABLE 1B. *Frequencies (in per cent) of X chromosome arrangements of* D. robusta *at North-South Woods, University City, Missouri, three miles east of Olivette*

Period	n	XL	XL-1	XL-2	XR	XR-1	XR-2
Sep. 25–28, 1946	316	98.1	0.6	1.3	35.8	61.4	2.8

divided into nine collecting periods; these are given in the left-hand column. The second column shows the number of chromosomes analyzed during each period. The data given represent combined egg samples and adult male samples.

During the year 1946, no significant changes occurred in the frequencies of the arrangements in the left arm. In 1947, the rare arrangements seem to be somewhat increased, although this increase is not significant. The tendency towards an increase over the 1946 levels, especially for XL–1, is indicated by the frequencies of June, 1948. Here XL–1 has a frequency of 2.7%, which, when compared with the combined frequencies for XL–1 in 1946–47, represents a significant increase ($P < .01$). This tendency appears to have been reversed in the fall of 1948, but the indicated reversal is not significant.

In the right arm of the X chromosome, despite some irregularity, there are no significant changes in frequency during 1946. There are no changes within 1947, but the overall 1947 frequency of XR–1 is significantly lower, and that of XR–2 higher, than in 1946 (P values well below .01). The concurrent increase in frequency of XR over the 1946 level is suggestive, but not significant ($P = .09$). These changed frequencies were maintained in 1948.

The data for the second chromosome are given in table 2A. 2L and 2L–1 showed no significant changes in 1946, but over the winter of 1946–47, 2L increased sharply and 2L–1 decreased. These changes are highly significant (P values near .01). Since the spring of 1947, both of these arrangements have returned to approximately the 1946 levels. In 2L–1, this return is accomplished during the summer of 1947, the increase from 30.3% in the spring to 38.0% in the fall being significant ($P = .04$). The corresponding decrease in 2L is more gradual.

TABLE 2A. *Frequencies (in per cent) of the gene arrangements in the second chromosome (left and right arms) and the third chromosome (right arm) of* Drosophila robusta *for the years 1946, 1947 and 1948 at Olivette, Missouri*

Period	n	Chromosome 2						Chromosome 3	
		Left arm				Right arm		Right arm	
		2L	2L-1	2L-2	2L-3	2R	2R-1	3R	3R-1
1946									
I. Mar. 5–Apr. 6	154	44.2	46.7	6.5	2.6	81.2	18.8	69.5	30.5
II. Apr. 13–May 15	245	51.0	38.8	7.3	2.9	81.6	18.4	69.4	30.6
III. May 18–Jun. 1	355	49.3	42.2	7.9	0.6	84.8	15.2	73.0	27.0
IV. Jun. 17–19	474	52.3	38.6	8.7	0.4	83.5	16.5	74.9	25.1
V. July 3–9	382	50.3	42.7	5.7	1.3	83.2	16.8	73.6	26.4
VI. July 23–Aug. 6	345	49.8	43.8	6.1	0.3	83.2	16.8	75.4	24.6
VII. Aug. 15–Sep. 3	297	46.5	42.7	9.1	1.7	82.5	17.5	72.4	27.6
VIII. Sep. 13–24	315	52.7	38.1	8.9	0 3	83.5	16.5	67.6	32.4
IX. Oct. 14–Dec. 10	220	49.5	37.3	12.7	0.5	85.0	15.0	62.7	37.3
1947									
X. May 19–Jun. 7	320	57.5	30.3	11.3	0.9	84.1	15.9	71.6	28.4
XI. Sep. 28–Oct. 17	316	53.5	38.0	8.5	0.0	83.2	16.8	67.4	32.6
1948									
XII. Jun. 5–14	588	50.8	39.1	9.2	0.9	83.3	16.7	68.0	32.0
XIII. Sep. 30–Oct. 9	210	51.9	37.6	10.0	0.5	80.0	20.0	66.7	33.3
Total I–XIII	4221	50.0	39.5	8.6	0.9	83.2	16.8	70.6	29.4

TABLE 2B. *Frequencies (in per cent) of second and third chromosome arrangements at North-South Woods, University City, Missouri, three miles east of Olivette*

Period	n	2L	2L-1	2L-2	2L-3	2R	2R-1	3R	3R-1
Sep. 25–28, 1946	316	63.0	30.1	6.3	0.6	78.5	21.5	68.4	31.6

The frequency of gene arrangement 2L–2 in periods I–VI in 1946 differs significantly from its frequency in periods VII–IX (P is near .01). The high level attained in late fall of 1946 has been maintained subsequently through 1947 and 1948. The slight drop in frequency in the fall of 1947 (11.3% to 8.5%) is not significant. A somewhat similar phenomenon is apparent in the frequencies of 2L–3. In 1946 it had a higher frequency in the early spring (periods I and II) than during the rest of the year ($P < .01$); its frequency has not changed significantly thereafter.

In the right arm of the second chromosome, the two alternative arrangements which are present have remained in a remarkably stable equilibrium throughout the three-year period (table 2A).

Table 2A also gives the data for the right arm of the third chromosome. As 3R and 3R–1 are the only gene arrangements occurring in this locality, a change in frequency of one is reflected in the frequency of the other. Viewing the data from the point of view of the frequencies of 3R–1, it will be noted that this arrangement appears to be high during the spring periods I and II of 1946, drops slightly during the summer and rises again in the late fall (periods VIII and IX). The first of these changes is on the borderline of significance (P is just above .05); the second, however, is highly significant ($P < .01$). Over the winter of 1946–47, the frequency of 3R–1 decreases significantly, dropping from 37.3% to 28.4% ($P = .03$). Since the spring of 1947, there have been no further significant changes. The slightly higher frequency of 3R–1 in the fall of 1947 might be taken as an indication that the 1946 event was being repeated, were it not for the fact that over the winter of 1947–48, and during 1948, the frequencies remained the same. There is thus little indication of a repeated cyclic change.

2. Frequencies at North-South Woods compared to those at Olivette

A single population sample was obtained at North-South Woods on the days immediately following collection VIII at Olivette (September 25 through 28, 1946). The frequency data derived from this collection are given in tables 1B and 2B. Chi-Square tests were made in order to compare the frequencies at North-South Woods with those at the Olivette Woods. The most profound differences are in the frequencies of 2L and 2L–1 (table 2B). The frequency of 2L at North-South Woods differs from its frequency in period VIII at Olivette Woods ($P < .01$) and from 2L in 1946 as a whole (P negligible). Comparable P values were obtained for 2L–1. In a number of other cases, the frequencies at North-South Woods are significantly different from those at Olivette, but the differences are not great enough or the samples large enough to test significantly against the frequencies of period VIII alone. In this category are the differences in 2R, 2R–1 and XR. In addition, several others (XR–2, 2L–2) are on the borderline of significance, that is, the P values are just above .05.

The salient points of the above observations may be summarized as follows:

(1) Arrangements 2L–2 and 2L–3 changed slightly in frequency at different times during the 1946 season. The arrangements in the right arm of the X chromosome were also involved in a significant frequency change over the winter

of 1946–47. In these cases, the changed frequencies were maintained subsequently, that is, during 1947 and 1948.

(2) The frequencies of 2L and 2L–1 changed reciprocally over the winter of 1946–47. Each subsequently returned to the 1946 level.

(3) 3R–1 increased (at the expense of its alternative, 3R) during the fall of 1946, and decreased again over the winter of 1946–47. There is little evidence that this cycle was repeated in 1947–48.

(4) 2R and 2R–1 did not change in frequency over the period studied.

(5) There is no evidence for progressive increase or decrease in frequency of any arrangement over the period studied.

(6) In September of 1946, the frequencies of the gene arrangements at the Olivette Woods were in a number of cases significantly different from the frequencies at North-South Woods, three miles distant.

3. Association of gene arrangement XL–2 with XR–2

Both XL–2 and XR–2 have low frequencies at Olivette (table 1A). Among the adult male samples obtained from this locality, only the group analyzed in June, 1948, contained any appreciable number of either of these gene arrangements. Of 106 males in this group, four carried XL–2 and five XR–2 (3.8% and 4.7%, respectively). All four XL–2 males also carried XR–2, although on a random basis considerably less than one such male would be expected. This association is highly significant (P negligible). A similar association exists in the adult male samples analyzed from the 1947 collections at Gatlinburg, Tennessee (Stalker and Carson, 1948), where both arrangements are more common than at Olivette. Of 75 males carrying XL–2, all were also XR–2, whereas only 60.3 would be expected on a random basis (P = about .01).

The data given above suggest that XL–2, when not in combination with XR–2, leads to inviability, at least in adult males. To further examine this point, the extensive data on the frequencies of the gene arrangements of *D. robusta* which are based on egg samples have been inspected for possible cases of the occurrence of XL–2 in the absence of XR–2. Egg samples are inefficient for testing this point, since most of the data are derived from smears of a single female larva from each inseminated wild female. When the X chromosome of any such test larva is heterozygous for arrangement in both arms, neither the parentage nor the association of the gene arrangements can be told. In a number of cases, however, the data were obtained from seven smears of male and female offspring of a given wild female or pair of wild flies. In most of these cases, inspection of the data permits the determination of the exact X chromosome types contributed by each parent. Six instances have been found in which XL–2 occurred in the absence of XR–2; five of these chromosomes occurred in the collections from Gatlinburg, Tennessee and the sixth from Leary, Georgia. In only one case, from Gatlinburg, was the chromosome (XL–2 : XR) clearly transmitted to the F_1 larva from the male parent. No other cases of the association of XL–2 with any other right arm arrangement have been found elsewhere, including Olivette. At this latter locality, XL–2 has been found in 33 instances among the egg samples; in no case did it occur in the absence of XR–2, despite the fact that the latter arrangement is itself rare in the population. Such a correlation seems highly significant.

Despite the almost exclusive association of XL–2 with XR–2, the latter arrangement has been found quite often in the same chromosome with XL and XL–1. The situation, therefore, may best be described by saying that whereas in most areas the occurrence of XL–2 depends almost entirely on its association with XR–2, XR–2 may occur frequently in the absence of XL–2.

The complete analysis of the chromosomal genotype of the adult male samples

permits not only the type of test described above, that is, for association between arrangements in the two arms of the *same* chromosome, but also for association of chromosomal arrangements *between* chromosomes. Accordingly, the following tests were made: second chromosome, left arm vs. second chromosome, right arm; second, left vs. third, right; second, right vs. third, right; second, left vs. X; second, right vs. X; third, right vs. X.

In all of the above cases, there was no deviation from random association. In view of this fact, the non-random association between XL–2 and XR–2 seems all the more significant. Several inferences may be drawn. In the first place, XR–2 may be looked upon as the "protector" of XL–2 in natural populations, in the sense that the presence of this latter arrangement is apparently limited to those areas where XR–2 is also present. Secondly, because of the similar relationship between these two arrangements in two such geographically separate areas as Gatlinburg, Tennessee, and Olivette, Missouri, it seems likely that the gene contents of these two arrangements may also be similar in the two places.

General Discussion and Conclusions

Even a cursory examination of the data given in tables 1A and 2A reveals that, on the whole, the gene arrangement frequencies of the Olivette, Missouri, population of *Drosophila robusta* were essentially constant over the three-year period studied. This is true both within and between years. The changes in frequency which have occurred are not repeated cyclic events but are either unidirectional changes, which are sustained thereafter, or changes which showed a subsequent reversal having no particular relationship to season.

Superficially, these findings appear to present quite a contrasting situation to that found in *Drosophila pseudoobscura* (Dobzhansky 1943, 1948) and *D. funebris* (Dubinin and Tiniakov 1945). In these two species, seasonal fluctuations in the incidence of certain gene arrangements have been found; the changes appear to follow the annual climatic cycle. What is important to remember in the present connection, however, is the fact that by no means all populations of these species show such seasonal changes. Thus, in *D. funebris,* cyclical changes in frequency occur in urban, but not rural areas. Similarly, certain populations of *D. pseudoobscura* (Dobzhansky 1943, 1948) show no seasonal changes, although this phenomenon occurs at nearby localities. No seasonal changes, furthermore, have been found in *D. persimilis* (Dobzhansky 1948). It is thus clear that even in a species in which seasonal variation in gene arrangement frequency has been described, this phenomenon does not occur universally. For this reason it is obvious that the lack of seasonal changes in a particular Missouri population of *D. robusta* does not preclude the possibility of seasonal changes at some other, as yet unstudied, locality.

The gene arrangement frequencies in populations of *Drosophila robusta* from different geographical areas differ greatly (Carson and Stalker 1947); many of them also differ over short distances where ecological change is great, as on a mountainside (Stalker and Carson 1948). These differences have been considered to be due to the differential action of natural selection, through varying ecological conditions, on the chromosomal types. The present study indicates that in a single geographical area, selection acts in such a way as to hold the chromosome arrangement frequencies at very precise levels over considerable periods of time. The mode of action whereby selection maintains such equilibria is not yet clear and will be the subject of further investigation.

Slight alterations in frequencies, such as have been observed, probably reflect adaptive responses to minor, non-cyclical changes in the environment. It seems fairly clear that these changes are not

due to genetic drift in greatly reduced populations, as many of the changes occur when the population is obviously at a high numerical level. Drift would furthermore be likely to affect all chromosome arms in which diversity of gene arrangement is found; this, however, is not the case, as few of the changes appear to occur simultaneously and certain frequencies are essentially stable throughout the period during which the population was studied. The minor but significant differences in gene arrangement frequencies at another woods, three miles distant from the main locality, may also reflect minor environmental differences between the two areas.

The considerations above, however, do not mean that seasonal adaptive changes do not occur in this species; on the contrary, we have shown in the accompanying paper that genetic changes in morphology occur despite the stability of gene arrangement frequencies (Stalker and Carson 1949). The general non-parallelism between morphological and cytological changes are discussed in the paper referred to, and will not be recapitulated here. It is noteworthy, however, that the altitudinal and seasonal studies are in accord on this point. In this connection, it may be pointed out that gene arrangements 2L–3 and XL–1, which have typically northern distributions in the eastern United States and both of which decrease sharply with altitude and latitude, may well contain genes adaptively associated with low-temperature environments. The fact that neither shows seasonal fluctuation might seem to negate this idea were it not for the fact that both are so rare in Missouri that even a 100 per cent increase would be very difficult to observe, due to sheer paucity of numbers. The very fact, moreover, that such rare arrangements are maintained in the natural population, despite their low numbers, indicates that they have some adaptive significance. For this reason, a study of gene arrangement frequencies in an area where one or both of these arrangements are abundant would be of considerable interest.

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Summary

1. The frequencies of various gene arrangements in a local population of *Drosophila robusta* near St. Louis, Missouri, have been followed over a period of three years. In this population, five chromosome arms show diversity of gene order.

2. A number of changes in frequency have been observed; they are slight and fall into two categories: (a) unidirectional changes which have occurred and have been sustained thereafter, and (b) changes which show a subsequent reversal, the frequencies returning to the original levels. Neither the original changes nor the reversals bear any consistent relationship to season of the year, and there is little evidence of cyclic change. There was no progressive increase or decrease in the frequency of any gene arrangement over the period studied.

3. In the fall of 1946, the gene arrangement frequencies present in a population three miles distant from the main collecting locality were recorded. In a number of cases, these frequencies differed significantly from those at the main locality.

4. Gene arrangement XL–2 has not been found in the absence of XR–2 in the Missouri population and, except for a few cases, the same relationship appears to hold in other geographical areas.

5. The general stability of gene arrangement frequencies in the population studied is considered to be maintained by natural selection.

6. The alterations and differences de-

scribed in (2) and (3) are considered to be due to an adaptive response, through natural selection, to slight alterations or differences in environmental conditions.

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OOLOGY

SEASONAL VARIATION IN THE MORPHOLOGY OF *DROSOPHILA ROBUSTA* STURTEVANT

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INTRODUCTION

In previously published studies of genetically controlled morphological variation in *Drosophila robusta,* Stalker and Carson (1947, '48) have shown that both north-south geographical clines and altitudinal clines exist. It has been demonstrated that in their broader aspects these two types of clines are parallel, with the morphological peculiarities of northern strains also found in strains from high altitudes, while southern strains resemble those from low altitudes. On the basis of this correspondence it seems probable that certain morphological characteristics may be adaptively associated with cool climates, while different characteristics would be adaptively associated with warm climates. If this were the case it would be possible that a population in one locality might adapt itself to the cyclic climatic changes associated with season, and undergo morphological change by a rapid type of natural selection. This change would presumably be toward a southern morphology during hot weather and toward a northern morphology in cold. Dobzhansky (1943, '47, '48a) has repeatedly demonstrated such seasonal fluctuations in *Drosophila pseudoobscura,* some of them undoubtedly due to natural selection, although in that species he followed changes in the frequencies of chromosome inversions, rather than changes in the morphology.

Timofeeff-Ressovsky (1940) has shown that in the beetle *Adalia bipunctata* the dark-colored form increases in frequency during the warm weather, while during the winter, when a large part of the overwintering population is killed, the light-colored individuals survive in the largest numbers. The proportion of light- to dark-colored individuals thus shows a cyclical change, this change apparently being caused by a rapid and vigorous natural selection.

In the present study we have attempted to answer three questions regarding seasonal morphological variation. 1. Is there genetically controlled seasonal morphological change within a population, and if so, what are its characteristics? 2. What is the probable direct (non-genetic) effect of the changing environment on the morphology of the wild population? 3. What part of the genetically controlled morphological variability is associated with specific gene arrangements found in the population?

MATERIALS AND METHODS

The population samples on which this study is based consist of collections of *Drosophila robusta* adults from a deciduous woods in Olivette, Missouri. Wild females, already inseminated in nature, or mated with a male caught at the same locality, and at approximately the same time, were allowed to oviposit in food vials in the laboratory. The F_1 individuals were reared at approximately 25° C. and after emergence were aged on fresh cornmeal-agar medium at 25.5° C. The food was changed every three days until the presence of large numbers of larvae indicated that the majority of the F_1 individuals in the vials were breeding. The flies were then placed in half-pint culture bottles together with a glass slide on which there was a slice of cornmeal medium, richly yeasted. After three days at 25.5° C. the food slice was examined under a binocular dissecting microscope, and 36 F_2 larvae removed with the aid of a blunt dissecting needle; the larvae being placed in another half-pint bottle along with one double sheet of cleansing

tissue and 16 cc. of fresh yeast suspension. This transfer was carried out in a 25° C. constant-temperature room. The development of the larvae then continued at 25.5° C. When the F_2 adults began to emerge they were removed from the rearing bottle at two-day intervals and kept on standard cornmeal-agar food for several days until they had hardened, after which they were killed with ether and preserved in alcohol for later measurement.

In the rearing method described above, the temperature was rigidly controlled but the humidity was not. Heuts (1948) has shown that in *D. pseudoobscura* different chromosome inversion types show significantly different pupal mortalities at low humidity. Thus critically dry culture conditions might exert a selective effect on *D. robusta* in that they eliminated certain genotypes differentially. Moreover, critically dry conditions might exert a direct effect-of-rearing on the phenotype. The humidity in the incubators undoubtedly varied during the course of the year, but in the course of routine examination of the bottles from which adults had emerged (as a check on pupal mortality), it was found that at all seasons the cleansing tissue was still "sopping wet." Since the pupae always formed in the cleansing tissue rather than up on the sides of the bottle, the environment immediately surrounding them must have been nearly saturated, and it seems very unlikely that any seasonal changes in morphology could have been the result of variations in the humidity of the culture medium.

The methods of measurement are described in our previous paper, Stalker and Carson (1947). All measurements were made with the aid of an ocular micrometer in which the micrometer reading "1.00" equals 483 micra. The mean measurements in the tables are expressed as these ocular micrometer readings.

In the present study the same five linear dimensions are compared as in the previous geographic and altitudinal studies, namely: thorax-length, head-width, femur-length, wing-length and wing-width. Five adult females were measured from each F_2 progeny; a total of 500 progenies, or 2,500 F_2 flies, were measured from the 1946 collection at Olivette, Missouri.

For convenience in handling the morphological data, the year's collections are referred to seven collecting periods. The extent of each period is indicated in table 1.

TABLE 1. *Seasonal means of 500 F_2 progenies from wild females captured in 1946. Five adult females measured in each progeny. All flies reared at 25.5° C.*

Collecting periods	No. F_2 progenies	Thorax-length	Head-width	Femur-length	Wing-width	Wing-length	Discriminant D_2*
I. Feb. 5–April 13	38	3.082	2.481	1.576	3.044	4.576	0.671
II. May 9–May 14	20	3.059	2.475	1.570	3.050	4.586	0.662
III. May 25–May 31	108	3.091	2.492	1.581	3.082	4.644	0.675
IV. June 17–June 19	100	3.080	2.486	1.580	3.060	4.624	0.671
V. July 3–July 6	100	3.091	2.499	1.577	3.064	4.620	0.658
VI. August 15–September 3	100	3.080	2.494	1.574	3.026	4.584	0.648
VII. Sept. 13–Sept. 17	34	3.076	2.480	1.566	3.031	4.576	0.656
Unweighted means for 1946:		3.083	2.490	1.577	3.055	4.611	0.663

* See text.

Results

Table 1 shows the period means for the five basic measurements. An analysis of variance indicated that in all cases the means of the F_2 progenies *within* each period constituted an heterogeneous group. On the basis of this finding, variance analysis was carried out in which the mean squares *between* periods were compared with the mean squares between F_2 progenies *within* periods. The results of these comparisons are summarized as the F-ratios in table 2.

In figures 1 and 2 the changes in mean seasonal measurements throughout the year are shown diagrammatically. In these figures the period means are shown as percentages of the yearly mean. Thus, for the first period, in the case of thorax-length (3.082) is 99.9% of the yearly mean thorax-length (3.083). In the second period the mean of 3.059 is 99.22% of the yearly mean, etc. By using these percentages rather than the raw means, the very considerable period-to-period changes in large dimensions, such as wing-length, are more directly comparable to the changes in small dimensions such as head-width and femur-length.

It will be noted from these figures that the seasonal changes in the five linear dimensions are roughly parallel. In other words, the most obvious seasonal change is one in over-all size. Since the seasonal changes for each measurement vary significantly, there is little doubt that the

TABLE 2. *Summary of tests of significance of seasonal differences for five basic measurements and the Discriminant Function, D_2 (see text)*

The figures in the table are F-ratios from analysis of variance. Those F-ratios which exceed that at the 1% level of significance are marked **, those which exceed that at the 5% level are marked *, and those which exceed neither are marked −. The variance ratios at the 5% and 1% levels are given at the right of each section of the table; the upper figure representing that ratio at the 5% level in each case.

Collecting periods compared	Variance ratios					Variance ratios at 5% and 1% levels	Variance ratios	Variance ratios at 5% and 1% levels
	Thorax-length	Head-width	Femur-length	Wing-length	Wing-width		Discriminant D_2	
All seven	3.34**	4.05**	2.69*	10.81**	15.41**	2.12 2.85	4.47**	1.90 2.45
I vs. II	3.69−	0.32−	1.11−	0.28−	0.17−	4.02 7.11	0.18−	2.39 3.39
I vs. III							0.04−	2.27 3.15
II vs. III	11.06**		3.91−			3.92 6.84		
II vs. V		9.99**				3.92 6.85		
I and II vs. III	6.19*	5.34*	0.72−	31.99**	23.11**	3.90 6.80	0.47−	2.27 3.13
III vs. VI	4.02*	0.33−	4.10*	39.71**	79.00**	3.89 6.76	6.34**	2.23 3.06
VI vs. VII	0.38−	5.72*	2.53−	0.39−	0.28−	3.92 6.83	0.35−	2.29 3.17

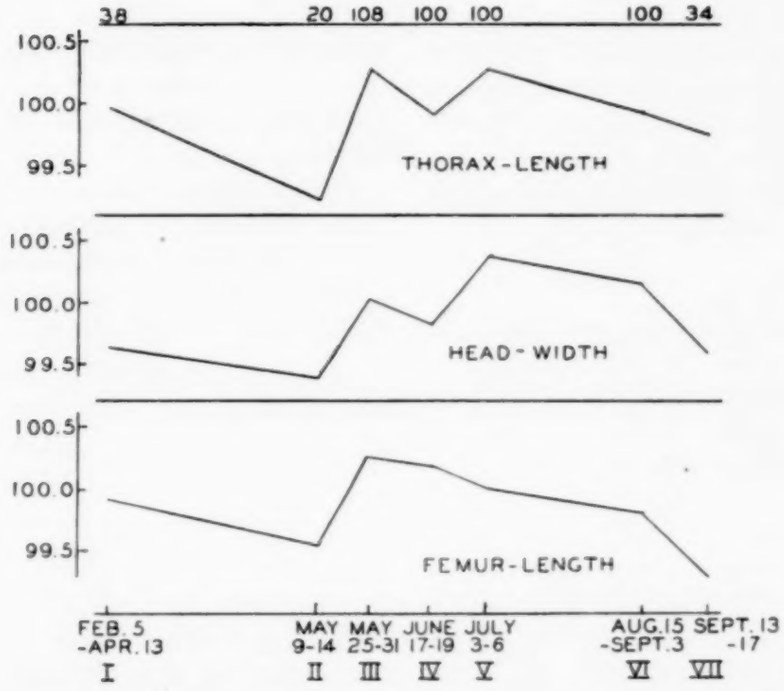

FIG. 1. Seasonal variation in thorax-length, head-width, and femur length of F_2 female progenies of wild females captured at various times in 1946. All measurements are based on laboratory-reared flies. The values for the period means are shown as percentages of the yearly mean (see text). The numbers along the top of the figure indicate the number of F_2 progenies on which each mean is based.

over-all size change indicated is also significant.

As mentioned earlier, we were particularly interested in determining whether or not the morphology of the adult flies underwent changes in a "northern" or

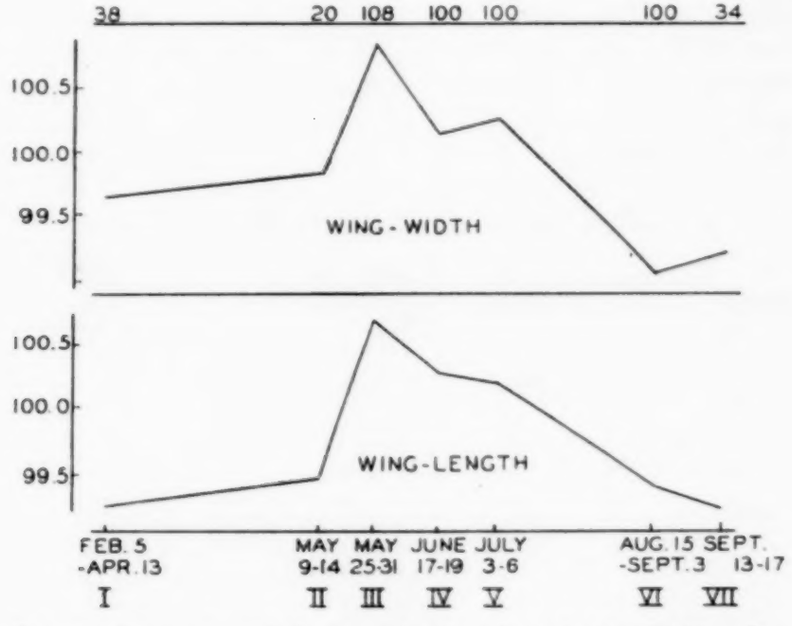

FIG. 2. Seasonal variation in wing-length and wing-width. See caption of figure 1 for further explanation.

"southern" direction during the course of the year. Our most efficient means of distinguishing northern and southern flies on the basis of their morphology is Fisher's Discriminant Function, Fisher (1936). The Discriminant Function is a compound measurement, such that:

$$D = c_1x + c_2y + c_3z + c_4u + c_5v,$$

where D is the compound measurement; x, y, z, u and v are the means of the five basic measurements, and $c_1 \ldots c_5$ are coefficients so chosen as to maximize the variance *between* groups being compared, relative to the variance *within* groups. Stalker and Carson (1947) chose coefficients so as to most efficiently discriminate between strains coming from seven different climatic zones in the United States.

The discriminant calculated (D_2 in our paper) then most efficiently indicated the over-all morphological differences between flies from different climatic zones. The D_2 values calculated for the 45 different geographic strains studied showed a highly significant negative correlation with average annual temperature of the strain source-locality. Thus, since the flies from the north had higher D_2 values than those from the south, a high D_2 may be considered as characteristic of a northern type of morphology, and the relative size of the D_2 values should therefore indicate the "northernness" or "southernness" of the morphology of any group of *D. robusta* adults. If, then, two groups of flies are compared morphologically, those with a significantly higher D_2 value should be considered as possessing a more northern phenotype than those with the lower D_2 value.

The five coefficients which led to the most efficient morphological discrimination between northern and southern strains were calculated in connection with the 1947 paper. They were:

thorax-length	$c_1 = +0.5030$,
head-width	$c_2 = -1.2630$,
femur-length	$c_3 = +1.0000$,
wing-width	$c_4 = +0.2193$,
wing-length	$c_5 = +0.0023$.

Using these coefficients with the mean period measurements for the five characteristics listed in table 1, a new set of discriminants was calculated which indicated the seasonal changes in the northernness or southernness of the morphology. These new discriminants are listed in the column headed "D_2" in table 1. The seasonal changes in D_2 are indicated graphically in figure 3.

Remembering that a high D_2 value is indicative of a northern phenotype, and a low one of a southern phenotype, it will be noted from figure 3, that the phenotype shows irregular fluctuations during the first three periods, then from periods III to VI there is a general trend in which the morphology becomes progressively more southern. Finally, the trend is reversed between periods VI and VII.

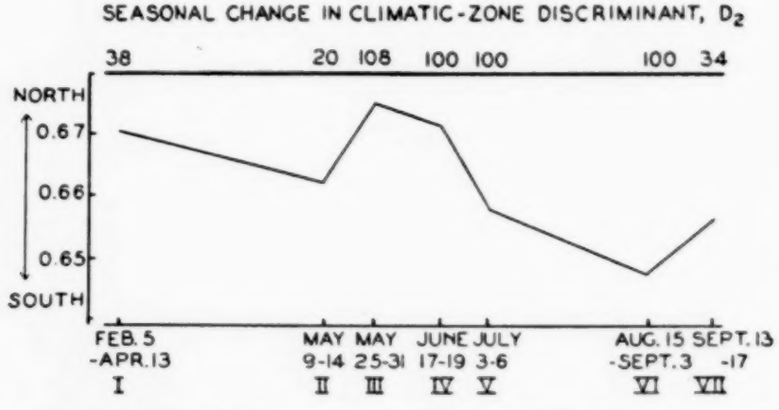

FIG. 3. Seasonal changes in the geographic Discriminant Function D_2. See caption of figure 1 and text for further explanation.

Table 2 summarizes the tests of significance for the seasonal differences in D_2. The results of these tests indicate that there is significant heterogeneity between the seven periods within the year, but that the changes in D_2 in the first two and in the last intervals are probably not significant. However, the considerable drop in D_2 between periods III and VI is highly significant, the difference between the values for these periods giving an F-ratio of 6.34 far exceeding the F-ratio of 3.11 at the 1% level of significance.

Thus it appears that the morphology does undergo a change toward the southern type during the warm part of the year, and that this change has a genetic basis.

Direct Effect of Rearing Temperature on Morphology

As indicated above, flies used in the measurements reported up to this point were all reared under standard laboratory conditions, at 25.5° C. Consequently, the changes in morphology could be ascribed to variation in the genotype. However, in nature flies develop under variable conditions of temperature, humidity, food supply, etc. Of these variables probably temperature is most easily controlled in the laboratory, and accordingly experiments were conducted to determine what direct non-genetic effect temperature of rearing might exert on the morphology of the adults.

Comparisons were made between flies

Table 3. *Morphological effects of rearing* D. robusta *at different temperatures. The means for the five basic measurements are given with their standard errors. In all cases 35 adult females were measured from the high temperature group, and 50 from the low temperature group.*

Strain	Rearing temp. ° C.	Thorax-length	Head-width	Femur-length	Wing-length	Wing-width	Discriminant D_2*
University, Alabama	17.6	3.334 ±0.0107	2.658 ±0.0063	1.703 ±0.0046	4.976 ±0.0183	3.326 ±0.0101	0.764
	25.5	3.107 ±0.0090	2.541 ±0.0081	1.579 ±0.0059	4.577 ±0.0177	3.077 ±0.0126	0.617
New Wilmington, Penna.	17.6	3.182 ±0.0096	2.548 ±0.0092	1.667 ±0.0053	4.954 ±0.0167	3.208 ±0.0124	0.764
	25.5	3.026 ±0.0092	2.432 ±0.0062	1.571 ±0.0040	4.495 ±0.0143	2.944 ±0.0093	0.677
Austin, Texas	17.6	3.232 ±0.0074	2.614 ±0.0047	1.644 ±0.0043	4.786 ±0.0120	3.210 ±0.0093	0.683
	25.5	3.026 ±0.0076	2.477 ±0.0033	1.537 ±0.0064	4.389 ±0.0197	2.941 ±0.0147	0.586
Rochester, New York	17.6	3.255 ±0.0089	2.599 ±0.0069	1.703 ±0.0063	5.081 ±0.0122	3.294 ±0.0083	0.792
	25.5	3.007 ±0.0083	2.421 ±0.0062	1.565 ±0.0052	4.469 ±0.0171	2.920 ±0.0107	0.671
Glen Ellyn, Illinois	17.6	3.185 ±0.0084	2.509 ±0.0056	1.661 ±0.0049	4.909 ±0.0133	3.181 ±0.0096	0.803
	25.5	3.024 ±0.0079	2.412 ±0.0053	1.573 ±0.0047	4.561 ±0.0147	2.993 ±0.0099	0.726

* See text.

TABLE 4. *Summary of tests for significance of differences between Discriminant D_2 values for flies reared at 25.5° C. and 17.6° C.*

Source of variation	d.f.	Mean squares				
		University, Alabama	Austin, Texas	New Wilmington, Penna.	Rochester, New York	Glen Ellyn, Illinois
A. Within temperatures	79	0.002990	0.002506	0.001719	0.002419	0.002213
B. Between temperatures	5	0.08892	0.03898	0.03098	0.06101	0.03273
Variance ratio, F, B/A		29.739	15.555	18.022	25.221	14.790

F value at 0.01 level of significance = 3.26.

reared at 25.5° C. and those reared at 17.6 ± 0.75° C. For such comparisons five strains from widely different geographical localities were tested; in each case the same group of parents was used for both the 17.6° C. and 25.5° C. cultures, so that both temperature groups should have been approximately alike genetically. In each strain measurements were made on 35 females reared at the high temperature, and 50 reared at the low temperature. The data for the 25.5° C. groups have been reported previously, Stalker and Carson (1947). The results of the morphological comparisons are shown in table 3. As might be expected, rearing flies at a lower temperature results in an over-all size increase, reflected in each of the basic measurements. Once again using the Discriminant D_2 mentioned above as a compound measure of the northernness or southernness of the morphology, we find that in each case the 17.6° C. flies have a higher D_2 value than those reared at 25.5° C. Table 4 shows that in each of the five strains the difference in the D_2 value is highly significant. Since a relatively high D_2 value is characteristic of a relatively northern phenotype, these results indicate that the temperature does exert a direct effect on the phenotype, and in the expected direction, since flies reared at low temperatures have a significantly more northern phenotype than those reared at high temperatures.

The objection might be raised that since four of the five coefficients associated with the Discriminant D_2 are positive (only c_2 for head-width being negative) this Discriminant is in fact nothing but a measure of over-all size. However, it should be noted, that although only one coefficient is negative, that coefficient is much larger than any of the four positive coefficients, and taking into account the average magnitude of the various dimensions with which these coefficients are associated, the single negative coefficient carries approximately 45% of the total weight. Moreover, even though the over-all size of the fly will certainly be reflected in the D_2 value, which in our data is always positive, this does not invalidate its use as a measurement of northernness or southernness of the phenotype, since our earlier findings on geographical variation in morphology indicate that over-all size is in fact one of the characteristics by which northern and southern flies differ.

It would be of some interest to know whether northern and southern strains differ in the degree of their reaction to temperature of rearing. The rise in the D_2 values associated with lowering of temperature is 0.147 and 0.097 for the two southern strains, and 0.087, 0.121 and 0.077 for those from the north. Thus, although a difference in reaction of northern and southern strains may exist, the data at hand give no clear indication of it.

CHANGES IN PROPORTION ASSOCIATED WITH TEMPERATURE OF REARING

The geographical variation in *D. robusta* involves not only differences in the

D_2 values, but associated with these differences are changes in proportion. Of these geographical changes in proportion those involving head-width and wing-length are the clearest and will be discussed below in connection with the temperature of rearing.

Studies of geographical strains of *D. robusta* have revealed that while wing-length has a significant negative correlation with average annual temperature of source locality, head-width has a significant positive correlation. Thus, a north-south difference exists in the proportion of head-width to wing-length with northern strains characterized by long wings and narrow heads, southern strains by short wings and wide heads.

In order to study the effect of temperature of rearing on this proportion the regression coefficients of wing-length on head-width within the ten temperature groups of the five strains were calculated. The ten regressions so obtained were not significantly heterogeneous. Furthermore, in none of the five strains was there a significant difference between the regression coefficients for the 17.6° C. temperature group and the 25.5° C. group. Using the strain mean regression coefficient in each of the five strains the adjusted mean wing-lengths for the 25.5° C. and 17.6° C. groups were calculated, the adjustment being made to the strain mean head-width. This adjustment was accomplished by the use of the formula: $Y = \bar{y} - b(\bar{x} - m)$, where Y is the adjusted mean wing-length for a particular temperature group, $\bar{y}$ is the unadjusted mean wing-length for that temperature group, b is the strain mean regression coefficient, $\bar{x}$ is strain mean head-width, and m is the temperature group mean head-width.

The strain mean head-widths and regression coefficients, as well as the original and adjusted wing-lengths, are listed in table 5. The differences between the wing-lengths of the two temperature groups, adjusted to a common head-width, are highly significant in each of the five strains, thus indicating that rearing at low temperature not only causes an in-

TABLE 5. *Comparison of adjusted values of wing-length. Mean wing-length of each temperature group is adjusted to mean head-width for each strain by use of strain mean regression coefficient of wing-length on head-width.*

Geographic strain	Temperature group	Strain mean head-width	Mean regression of wing on head	Unadjusted wing-length	Adjusted wing-length	Diff. in adjusted wing-lengths	Standard error of difference	t
University, Alabama	17.6° C.	2.610	1.1731	4.976	4.920	0.262	±0.0235	11.149
	25.5° C.			4.577	4.658			
Austin, Texas	17.6° C.	2.558	1.1808	4.786	4.720	0.235	±0.0182	12.912
	25.5° C.			4.389	4.485			
Rochester, New York	17.6° C.	2.526	1.0287	5.081	5.006	0.429	±0.0178	24.101
	25.5° C.			4.469	4.577			
New Wilmington, Penna.	17.6° C.	2.500	0.8724	4.954	4.912	0.358	±0.0207	17.295
	25.5° C.			4.495	4.554			
Glen Ellyn, Illinois	17.6° C.	2.469	1.0753	4.909	4.866	0.244	±0.0183	13.333
	25.5° C.			4.561	4.622			

$t = 2.636$ at 1 per cent level of significance.

crease in northernness as indicated by the D_2 value, but also causes a change in proportion of head and wing similar to that found in northern geographical strains, with the low temperature flies showing long wings and relatively narrow heads, and the high temperature group having the reverse proportion.

Correlation of Morphology and Gene Arrangements

Parallel studies of geographical and altitudinal variation in inversion frequencies and morphology (Stalker and Carson, 1947, '48; Carson and Stalker, 1947) have shown that in both the inversion frequencies and morphology, north-south geographical and high-low altitudinal clines exist. Since chromosome inversions tend to trap blocks of genes, it would seem that one way in which the genetic basis of the morphology might be controlled, would be by adjustment of the various inversion frequencies. Such an adjustment would be effective only if some of the genes controlling the morphology were in fact included in or lying near the various inversions.

The altitudinal study revealed that although over-all morphology of high-altitude flies was "northern" relative to that of low-altitude flies, there was not a general tendency for the "northern" gene arrangements to show the highest frequencies at high altitudes, and "southern" arrangements the highest frequencies at low altitudes. Moreover, the regions in the altitudinal transect which gave the sharpest changes in the gene arrangement frequencies were not those which showed the sharpest changes in the morphology. These facts seemed to indicate that whatever the relationship between the gene arrangements and morphology, it was not a simple one in which geographically "northern" arrangements were responsible for a "northern" phenotype, and "southern" arrangements for a "southern" phenotype.

In neither the geographical nor the altitudinal studies was it possible to make any direct tests of correlation between gene arrangements and morphology since the populations studied were so variable cytologically that large numbers of strains would have been needed in order to study the effect of any particular gene arrangement. In fact the numbers of strains from any one locality known both cytologically and morphologically were very small. However, in the present study since all of the F_2 progenies used were descended from F_1 progenies, some of the members of which were analyzed cytologically, attempts have been made to correlate the morphology of the various F_2 progenies with whatever cytological information was available. In each case at least one F_1 female individual was analyzed cytologically, thus giving the information on half of the chromosomes from each of the two wild parents. Thus for each F_2 progeny half of the chromosomes of the grandparents were known. Even with such limited cytological information, a group of F_2 progenies in which the known left arms of the second chromosomes of the grandparents were, for instance, both 2L, should on the average contain more 2L arrangements than F_2 progenies in which the known chromosomes of the grandparents were both 2L–1. Consequently if the 2L and 2L–1 arrangements had sufficiently different effects on the morphology it might be expected that a significant morphological difference would exist between the two groups of F_2 progenies.

So much cytological diversity was found to exist in the seasonal material from Olivette, Missouri, that it was impractical to consider all of the known chromosomal contributions of the grandparents at one time. Rather, one pair of alternate chromosome arrangements was considered in any one comparison. Since it has been shown above that seasonal morphological variability exists, comparisons between any two groups of F_2 progenies were made between groups *within* collecting periods.

Most of the inversion types encoun-

TABLE 6. *The seasonal means and Discriminant D_4 for each of the five basic measurements for F_2 progenies with known X chromosomes both XR or both XR-1, respectively.*

Season	Known chromosomal constitution	No. F_2 progenies	Thorax-length	Head-width	Femur-length	Wing-length	Wing-width	Discriminant D_4 (see text)
III	Both XR	20	3.096	2.494	1.584	4.671	3.092	0.686
	Both XR-1	27	3.080	2.486	1.576	4.619	3.071	0.663
IV	Both XR	14	3.086	2.489	1.592	4.632	3.062	0.690
	Both XR-1	35	3.079	2.485	1.578	4.631	3.064	0.685
V	Both XR	16	3.088	2.498	1.578	4.653	3.069	0.702
	Both XR-1	30	3.089	2.498	1.577	4.611	3.063	0.668
VI	Both XR	23	3.087	2.497	1.577	4.591	3.033	0.691
	Both XR-1	31	3.074	2.490	1.575	4.569	3.024	0.681

tered during the seasonal analysis did not lend themselves to correlation with the morphology, since, due to their rarity, it was not possible to find sufficiently large numbers of F_2 progenies of the various chromosomal types to make adequate comparisons.

The four sets of gene arrangements which, on the basis of numbers available, showed the most promise were: XR vs. XR–1; 2L vs. 2L–1; 2R vs. 2R–1 and 3R vs. 3R–1.

Arrangement XR vs. XR–1

Sufficient numbers of F_2 progenies with known X-chromosomes both XR or both XR–1 were available for comparison in collecting periods III, IV, V, and VI.

Table 6 shows the mean for each of the five basic measurements for each of the two groups of progenies in these four collecting periods. Table 7 summarizes the tests of significance, and indicates that four of the five basic measurements showed no significant differences in the

TABLE 7. *Comparison of F_2 progenies with known X-chromosomes both XR and those with known X-chromosomes both XR-1. Summary of tests of significance for five basic measurements and Discriminant D_4. 196 F_2 progenies, 5 flies per progeny, 4 seasons, 2 chromosome groups in each season.*

Source of variation	d.f.	Mean squares					d.f.	Mean squares
		Thorax-length	Head-width	Femur-length	Wing-length	Wing-width		Discriminant D_4 (see text)
A. Within F_2 progenies	784	0.002426	0.001445	0.000926	0.007083	0.002965		
B. Between progenies within chromosome groups	188	0.007410	0.004517	0.002532	0.025185	0.011860	172	0.001166
C. Between chromosome groups within seasons	4	0.006950	0.001950	0.003400	0.070875	0.008250	20	0.005175
F-ratio B/A		3.054**	3.126**	2.734**	3.556**	4.000**		
F-ratio C/B		0.938–	0.432–	1.343–	2.814*	0.696		4.438**

Those F-ratios marked ** exceed that at the 1 per cent level of significance; those marked * exceed that at the 5 per cent level; those marked – are less than that at the 5 per cent level.

pooled within-collecting-period comparisons between the two chromosomally different groups. For wing-length the F-ratio of 2.814 exceeded the ratio 2.41 at the 5% level of significance. Reference to table 6 shows that the wings of the XR group are longer than those of the XR–1 group in all collecting periods, although this difference is clearly not significant in period IV. The probable significance of the pooled differences indicates that XR is associated with longer wings than XR–1. A new Discriminant Function, D_4, was calculated such that the variance between progenies within chromosomal groups would be minimal compared to the variance between groups within collecting periods. The coefficients for D_4 turned out to be:

thorax-length	$c_1 = -0.0867$,
head-width	$c_2 = +0.2278$,
femur-length	$c_3 = +0.0901$,
wing-width	$c_4 = -1.4320$,
wing-length	$c_5 = +1.0000$.

Using the means of the basic measurements given in table 6 a mean D_4 for each chromosomal group within each period was calculated, and these values are listed in the last column of table 6. It will be noted that for each of the four periods the D_4 value is higher for the XR than for the XR–1 group. The test of the significance of the pooled differences within the four periods is indicated in table 7, and shows that the differences are highly significant. Thus it appears that the gene arrangements XR and XR–1 are associated with differences in morphology which are evident on the basis of wing-length alone, but are much clearer when all five morphological characters are considered together, as in the Discriminant D_4.

Arrangement 2L vs. 2L–1

Comparisons between F_2 progenies whose known second chromosomes were both 2L or both 2L–1 were made over periods III, IV, V and VI; the 2L group being represented by a total of 87 progenies, the 2L–1 group by 67 progenies. In none of the five basic measurements were there significant inter-group differences within collecting periods. A Discriminant Function was calculated which would best discriminate between the two groups, but the test of significance of the pooled intra-period comparisons for this function gave an F-ratio of only 1.07, considerably less than the F-ratio 2.03 at the 5% level of significance. Thus evidence that 2L and 2L–1 are associated with differences in morphology is lacking.

Arrangement 2R vs. 2R–1

Since few F_2 progenies whose known second chromosomes were both 2R–1 were available, comparisons were made between 287 progenies with known second chromosomes both 2R, and 108 with known second chromosomes 2R and 2R–1, over four collecting periods. In none of the five basic measurements were there significant inter-group differences within periods. A Discriminant Function calculated to best discriminate between the two groups gave an F-ratio of 0.41 for the pooled intra-period comparisons, well below the F-ratio 1.60 at the 5% level of significance. Thus evidence is lacking that 2R and 2R–1 are associated with differences in morphology.

Arrangement 3R vs. 3R–1

Due to scarcity of the desired types of F_2 progenies, comparisons were made between 160 progenies with known third chromosomes 3R and 3R–1, and 221 with known third chromosomes both 3R–1, over four collecting periods. As in the two cases above, the means for each of the five basic measurements showed no significant inter-group differences. The most efficient Discriminant Function which could be calculated to distinguish the two types of progenies showed an F-ratio of 0.33, well below the F-ratio 1.60 at the 5% level of significance.

Since the comparative technique used was rather inefficient, the three comparisons reported immediately above are certainly not critical, and must be considered

as offering lack of evidence, rather than negative evidence that the arrangements 2L, 2L–1; 2R, 2R–1; 3R and 3R–1 are associated with morphological differences.

The fact that the first comparison reported, that involving XR and XR–1, showed significant differences while the other three did not may be due partly to the fact that in dealing with the X-chromosomes, information was available on two out of the three X-chromosomes in the F_2 progeny, while in the case of autosomal comparisons only two out of the four autosomes were known. Thus, progenies to be tested could be classified much more accurately in regard to their X-chromosomes than for their autosomes.

XR and XR–1 show no clear trend in relative frequency changes as one passes from north to south geographically, although they do show a fairly clear east-west change, with XR "eastern" and XR–1 "western." Consequently it is not surprising that use of the north-south discriminant D_2 is of little help in distinguishing the two chromosomally different groups of F_2 progenies. In fact when a D_2 was calculated for each group within each period it was found that it gave a non-significant difference between the two groups, indicating that the groups do not differ significantly in the northernness or southernness of their morphology.

Discussion

The seasonal changes in morphology observed in this study show striking parallelism with the morphological changes observed in the altitudinal and geographical studies. Thus, in the spring the morphology of the St. Louis population tended to resemble northern or high altitude strains; during the course of the summer it gradually changed until by the end of the hot weather it had become morphologically more southern or low altitude. If the northernness or southernness of the morphology actually has adaptive value, or is associated with physiological adaptiveness (and the regularity and parallelism of the geographical and altitudinal clines strongly suggests that it is in some way adaptive), then the observed warm-weather changes in the St. Louis area are exactly what would be expected as a result of natural selection, with the southern or low altitude genotypes replacing the northern or high altitude genotypes. Whether or not the changes observed in 1946 represent regularly repeated cyclical changes it is impossible to say. However, unless the observed changes represented part of a long term more or less permanent change in the morphology, it would seem likely that the morphology should revert to its original spring characteristics during the following winter.

The change in the morphology-controlling genotype of the population during the summer of 1946 (whether or not as a result of natural selection), is in marked contrast to the relative stability of the chromosome inversion frequencies. Such dissimilarity of the chromosomal and morphological changes is not new: in the study of the altitudinal transect both inversion frequencies and morphology changed with altitude, but more or less independently of each other. The observed chromosome inversions cover a large part (approximately fifty per cent) of the euchromatic material, and it is clear that inversions are not wholly without morphological effect (see above); thus the possible role of the inversions in the seasonal genotypic changes cannot be disregarded.

It is of course probable that some of the genes controlling the observed morphological changes may lie outside the limits of the inversions, and hence could assort independently. On the other hand, as pointed out in the altitudinal study, changes of gene frequencies within the limits of the seemingly stable inversions are not ruled out.

Dobzhansky (1948b) has evidence that in *D. pseudoobscura* chromosomes with the same gene arrangement may have different genetic values. In our own case the gene arrangement 3R–1, for example, may well include considerable genetic

heterogeneity. Genetically different 3R–1 chromosomes would tend to become similar only to the extent that they occurred together in the homozygous condition, and in the case of rare gene arrangements the frequency of homozygotes would be very low. Genetically different chromosomes with the same gene arrangement would then be partially isolated in a population and might offer opportunities for selection of blocks of genes, and a rapid change of genotype. If, for example, such heterogeneity did exist in 3R–1 in *D. robusta,* then the frequency of 3R–1 relative to the alternate arrangement 3R, would be maintained by the action of selection on a group of genes common to all chromosomes of the 3R–1 arrangement which were different from genes found in all chromosomes of the 3R arrangement. Thus, the frequency of the arrangement 3R–1 might remain constant, while the frequencies of the various genetic *types* of 3R–1 could vary widely.

We have assumed above that the genotypic changes observed were under the influence of natural selection. However, in populations with a small effective breeding size genetic drift might be a much more important factor in causing rapid genetic change, and we have no information on the effective breeding size of *D. robusta* populations. Nevertheless, if genetic drift were an important factor in changing the gene frequencies, it should also act to change inversion frequencies. Yet, as noted above, the inversion frequencies were remarkably stable throughout. This would indicate that the population sampled was effectively large enough so that genetic drift was not an important factor.

If genetic drift is not responsible for the observed changes, it becomes very difficult to find any other reason why the genotype should change during the summer in such a regular way unless in response to natural selection.

Thus, it appears that *D. robusta* may adjust the morphology to the environment in three different ways. 1. It may differentiate into genetically diverse altitudinal or geographic strains. 2. It may undergo rapid genetic adjustment within one locality in response to local seasonal conditions. 3. It may undergo a direct, non-hereditary change in phenotype in response to the temperature of rearing.

Of these three methods of adjustment of morphology, it seems probable that the last would be the most efficient, since selection in this case tends to be unidirectional, that is, there is a continuous selection for genes conferring a particular type of developmental plasticity on the species. In the case of periodic genetic adjustment, selection must be reversed in direction twice a year, with a correspondingly wasteful elimination of first "northern" and then "southern" types of individuals.

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Summary

A study of genetically controlled seasonal variation in morphology was made of a natural population of *Drosophila robusta* near St. Louis, Missouri. Five hundred F_2 progenies from wild flies captured in the period from February to September 1946 were reared under uniform laboratory conditions, and five adult females were measured from each progeny.

Of the five characters measured, thorax-length, head-width, femur-length, wing-length and wing-width, all showed significant seasonal heterogeneity. Using the compound measurement D_2 (Fisher's Discriminant Function), as an indication of northernness or southernness of the morphology it was shown that the population underwent a regular, highly significant shift toward a southern morphology during the summer months June through August. This shift during the hot weather was in the direction expected

if the southern morphology has high-temperature adaptive value, and if the species undergoes a rapid selective response to seasonal temperature fluctuations. The seasonal changes in morphology are in marked contrast to the essential stability of the gene arrangement frequencies. Since such stability seems to indicate a relatively large breeding population it is felt that the observed morphological changes cannot be attributed to genetic drift, and are probably the result of natural selection.

In order to determine the direct, non-genetic effect of the temperature of rearing on the morphology, five geographically diverse strains were used in which flies reared at 25.5° C. and those reared at 17.6° C. were compared morphologically. It was found that the low temperature group were more northern in their morphology than those reared at high temperatures. The northernness of the low temperature group was indicated both by their D_2 values and by the typically northern shift in the proportion of head-width and wing-length.

By comparing the F_2 progenies coming from wild parents carrying different gene arrangements it was shown that the arrangements XR and XR–1 are associated with different morphological characteristics.

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EVOLUTIONARY CHANGES IN THE SEX CHROMOSOMES OF COLEOPTERA. I. WOOD BORERS OF THE GENUS *AGRILUS* [1]

STANLEY G. SMITH [2]

INTRODUCTION

A review of the literature (Harvey, 1916, 1920; Suomalainen, 1940a) and an extensive sampling of species representing 18 families of beetles establishes the fact that there are at least four types of sex-determining mechanisms operating in the Coleoptera. These are: (1) haploid-(♂)-diploid(♀), known only in *Micromalthus debilis* Lec. (Scott, 1936); (2) XO(♂)-XX(♀) and (3) XY(♂)-XX(♀), as exemplified by the pioneer work of Stevens (1905, 1906, 1908, 1909), and more recently that of Suomalainen (1940a and b, 1947); and (4) a multiple condition involving five chromosomes in *Blaps lusitanica* Hbst. (Nonidez, 1920; Wilson, 1925). An XXO(♂) system, resembling that of spiders (Painter, 1914; Revel, 1947; Pätau, 1948), has been reported for various species of *Cicindela* by Goldsmith (1919), but his account is very unsatisfactory and conflicts with that of Stevens (1906, 1909).

Of the species known to the writer 21 fall into the XO category and 82 into the XY. Of the latter only eight were known prior to the present study to have a Y chromosome which approaches the X chromosome in size. Three are scarabaeids (Prowazek, 1902; Hayden, 1925) and one a coccinellid, *Cleis hudsonica* Csy. (unpub.), in all of which there is no heteromorphism in the sex pair; the fifth is a lagriid, *Arthromacra aenea* (Say), with a slight but consistent inequality between the X and Y (unpub.), and the remainder are buprestids in which both X and Y are large but definitely unequal in size (Asana, Makino, and Niiyama, 1942). Otherwise, striking differences in the sizes of the X and Y chromosomes result from the small size of the Y, which often approaches the lower limit of visibility. Furthermore, the two chromosomes usually have median centromeres and are associated at the first meiotic metaphase by means of two terminal points of association. The resulting configuration then bears a strong resemblance to a "parachute," as was remarked by Stevens (1906) in her description of the chrysomelid *Odontota dorsalis* (= *Chalepus dorsalis* Thunb.). How general association of this type is in XY species is difficult to determine from the illustrations published by the earlier workers. It is a fact, however, that, apart from the cicindelids and *Blepharida rhois* (Forst.) (Stevens, 1906), two meloids and a hydrophilid (Asana, Makino, and Niiyama, 1942), and a species of *Silpha* and one of *Quedius* (both unpub.), there is remarkable uniformity in the appearance of the sex pair in XY species. There can, therefore, be little doubt that the parachute type is the primitive system in the order, the XO and X-largeY being derivative systems.

The XO system has arisen on many occasions in the phylogeny of the order. It is found in at least six families, five of which possess other members with X-minute-Y sex-determining chromosomes. Mechanically, the surviving X chromosome has evolved in two directions. In five of the families it behaves, as does the univalent X of the Acrididae, by going undivided to the pole at the first anaphase and dividing equationally at the second. In the sixth family, the Lampyridae, some genera show this behavior (unpub. data), but in two others, *Photinus consanguineus* Lec. and *Photuris pennsylvanica* (DeG.) (incorrectly reported as *Photinus pennsylvanicus* by Stevens, 1909), the X divides at the first and not the second anaphase.

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It has been plausibly argued (Darlington, 1939a; White, 1945) that the more primitive organisms had X and Y chromosomes that were morphologically similar and that the more advanced types show an increasing degree of difference. If such were the case in the Coleoptera, it would appear that there now remain no representatives of this hypothetical type or that the order arose after the parachute condition was established, for we can hardly entertain the idea of *Cleis, Arthromacra,* and others as remnant species. It is difficult to escape the conclusion that previously autosomal material has become incorporated in the sex chromosomes in these species. The process which gave rise to this condition could have been similar to that responsible for the neo-XY system found in the three Indian buprestids (see Discussion). Evidence that such "fusion" between autosomes and sex chromosomes has occurred in the evolution of another X-largeY coleopteran forms the subject matter of the present paper.

Material and Methods

Two closely related species of wood borers (Buprestidae), currently referred to the species *Agrilus anxius* Gory, have been shown by Barter (unpub.) to be separable on the basis of differences in genitalic characters. One is restricted to *Betula,* the other to *Populus.*

Specimens were provided by Mr. G. W. Barter of the Dominion Entomological Laboratory, Fredericton, N. B. The abdomens of adults were opened ventrally and the exposed cavities forcibly flooded with modified Kahle's fluid. The gonads were then transferred to fresh fixative for two to three minutes, placed in a drop of 45 per cent acetic acid on an albumenized slide, covered, heated, and flattened with considerable pressure (Smith, 1943). Alternatively, the dissected and fixed gonads were run up through an ethyl-butyl alcohol series (Smith, 1943) and embedded in paraffin. Sections were made at 14 microns and all staining was done by the Feulgen-light green method (16 min. hydrolysis at 60° C.; 1 to 2 hr. Feulgen). Males four to six days after eclosion provided all stages of meiosis but very few spermatogonial divisions. For these and oogonial mitoses specimens were used one or two days after pupation.

All drawings were made at an original magnification of × 4,400 with the aid of a *camera lucida,* using a Zeiss 1.5 mm. 1.3 N.A. apochromatic oil immersion objective and a × 20 eyepiece. They are reproduced here at a magnification of × 3700 unless otherwise stated.

Observations

(a) *The Birch Borer*

In spermatogonial metaphases, males of the birch borer have 21 relatively large chromosomes and a single, minute, spherical one (fig. 1). The position of the centromere in the large chromosomes is median or almost so. Its position in the smallest chromosome cannot be ascertained at this stage because of the small size of the chromosome. At late prophase, however, it is seen to be median and confirmation is supplied by the appearance and behavior of this chromosome at the first meiotic metaphase. In oogonial metaphases birch borer females have 22 large, more or less V-shaped chromosomes, similar to the larger ones in the male; there is no minute spherical element (fig. 2). The latter chromosome in the male is, therefore, the Y member of the XY sex-determining pair, the X being

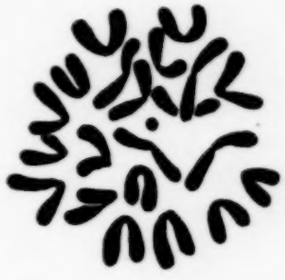


Fig. 1. Birch borer spermatogonial metaphase: 20 autosomes, an indistinguishable X and a minute y chromosome.

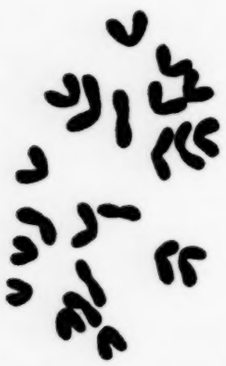


FIG. 2. Birch borer oogonial metaphase: 20 autosomes and 2 indistinguishable X chromosomes.

one of the larger chromosomes, though indistinguishable from the autosomes. In view of the small size of the spherical chromosome, both in relation to the X and compared with the Y of some other beetles, it will henceforth be designated as the "little y" chromosome, and the sex chromosome pair designated as Xy. The complements of the birch borer may, therefore, be symbolized as 20A + Xy (male) and 20A + XX (female).

As is frequently the case with the sex elements in the heterogametic sex (Stevens, 1905, 1906, 1909), the X and y exhibit heteropycnosis in the resting stage of at least some somatic cells (fig. 3a).

a b

FIGS. 3a and 3b. Somatic resting stages in birch and poplar males respectively showing relative sizes of heteropycnotic bodies.

Whether this holds also for the resting stage in spermatogonia has not been determined, as full resting stages have not been seen with certainty. It seems improbable, however, as supercondensed bodies are absent throughout spermatogonial prophase. Strong heteropycnosis is next evident during the meiotic prophase. At pachytene the sex pair is closely associated with the nucleolus and takes the form of a highly condensed and usually deeply-staining sphere (fig. 4a). Occasionally the staining is less intense in the center but the periphery remains unaffected as has been illustrated by Stevens (1909, figs. 38 and 56). Also, at

a b

FIGS. 4a and 4b. Pachytene in males of the birch and poplar borers respectively. In both there is association between the heterochromatic sex chromatin and the nucleolus. In 4a the sex chromosomes are totally heterochromatic; in 4b they are heterochromatic and euchromatic.

this stage a procentric initiation of condensation is often visible in the autosomes. In the females, the two X chromosomes fail to show a differential behavior in the somatic, gonial, and meiotic prophases and the resting stages.

At the first metaphase of meiosis (fig. 5) in the male the 10 pairs of autosomes, closely resembling dumb-bells in shape, line up on the equatorial plate. Although the autosomes are more or less equal-

FIG. 5. First metaphase in birch borer male: 10 autosomal bivalents and the heterochromatic Xy pair.

armed, as seen at spermatogonial metaphase, the exact nature of their association cannot be determined as a result of their small size and excessive condensation. However, in view of their symmetry and subsequent behavior and the fact that they can sometimes be seen to be ring-shaped, they presumably possess two terminal points of union, one in each arm. The Xy pair, which earlier showed strong positive heteropycnosis, by metaphase stains slightly less intensely than the autosomes; that is, it is negatively heteropycnotic. Furthermore, this pair is usually, if not always, late in congression; unlike the autosomes it at first lies slightly off the plate and with the smaller member closer to it—orientation is first achieved, congression follows. Association between the X and y is invariably by two terminal contact points, one in each arm.[3] It is the attenuation at these two points of contact, together with the extreme size difference between the X and y, that gives this bivalent its characteristic parachute-like appearance. Three factors then, their distinct shape, their differential staining, and their delay in congression, facilitate the detection and identification of this sex pair (fig. 5). With the subsequent alignment of the Xy bivalent on the equator, the component chromosomes of all pairs disjoin and proceed to opposite poles. Disjunction is thus invariably reductional for the structural inequalities in the Xy pair.

At metaphase in secondary spermatocytes the 10 autosomes and the single sex chromosome line up on the equatorial plate, with neither the X nor the y showing delay. Two types of metaphase occur: one with 11 V-shaped chromosomes of approximately equal size, the other with only 10 V-shaped chromosomes and one minute spherical element (fig. 6).

FIG. 6. Daughter second metaphases in birch borer male: 10 + X and 10 + y.

No other type of complement occurs. An equational division at anaphase gives, with similar sets of chromosomes going to opposite poles, either 11 V-shaped or 10 V-shaped and a small round one. Young

[3] Because of the nature of the material, observational evidence that the two terminal unions between the X and y chromosomes are the result of chiasma formation is lacking; in fact, it is only by inference that the associations between autosomal pairs can be considered to be chiasmata. Chiasmata are, however, clearly demonstrable in the autosomes of those Coleoptera that are amenable to study at prophase, but no indisputable evidence is available concerning the sex chromosomes in the heterogametic sex. If the sex chromosomes are associated by chiasmata, then, in view of their condensed state at the time that chiasma formation is presumably occurring in the autosomes, it would appear that the sex chromosomes must either achieve this exchange under different conditions of spiralization or pre-date the autosomes in chiasma formation. In the absence of direct evidence of either crossing over or chiasma formation in the borers dealt with here, it appears preferable to discuss terminal unions between chromosomes in terms of pairing segments, rather than chiasmata. Thus, the contact points between the arms of the X and y chromosomes are considered to indicate the presence in this pair of two pairing segments because in three species of beetles in different families the X and y chromosomes, of a size comparable to those in the birch borer, are invariably associated at first metaphase by a single, terminal point of contact. Those between the autosomes, however, might reasonably be considered to be terminalized chiasmata because in elaterids, whose chromosomes are larger, bivalents are present at metaphase with and without contact points between one of the two pairs of arms and the former may or may not be terminal. Whether there are pairing segments in the X and y that form chiasmata does not, of course, vitally affect the general argument.

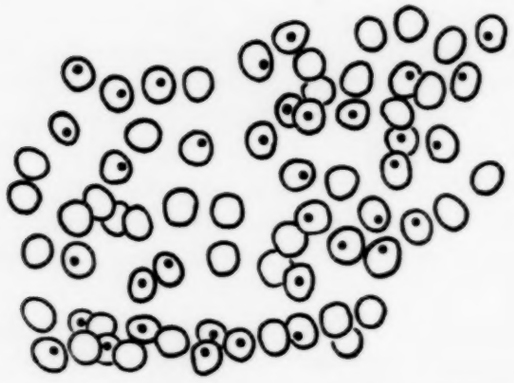
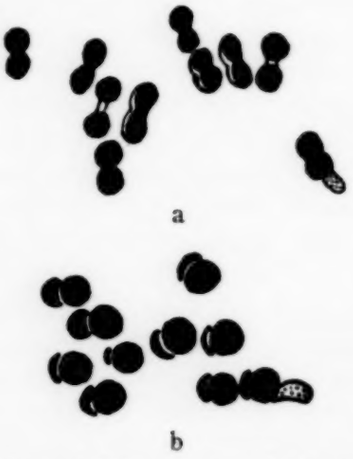


FIG. 7. Birch borer spermatids: approximately equal numbers with and without a heterochromatic body × 2000.

spermatids, with and without a large heteropycnotic body, occur in equal numbers (fig. 7). Obviously, those with this body are X-containing; those without, y-containing. It is highly probable that the y chromosome in the latter category is likewise heteropycnotic, but its small size makes its identification impossible.

(b) *The Poplar Borer*

Poplar borers differ from birch borers in having a lower chromosome number. Males have a total of only 20 chromosomes, all more or less V-shaped in spermatogonial metaphases, the small, spherical y seen in birch borer males being absent (fig. 8). Similarly, females show only 20 more or less mediocentric chromosomes in oogonial mitoses (fig. 9). In the male, however, one chromosome is about 50 per cent longer than the others, clearly because of the excess length of one arm. Two of these longer chromosomes are present in the female. The invariable relationship between the number of this type of chromosome and sex shows it to be the X chromosome in this borer, the other sex chromosome being one of the smaller V-shaped ones. We may, therefore, symbolize the complements of the two sexes as 18A + XY for the male and



FIGS. 10a and 10b. First metaphases in poplar borer males: 9 autosomal bivalents and the composite sex bivalent. 10a, side view; 10b, polar view.

18A + XX for the female, using in this case a capital Y to emphasize the larger size of this chromosome in contrast with the y of the birch borer male.

Positive heteropycnosis is manifested by the male at the resting stage in somatic nuclei (fig. 3b) and in early meiotic prophase; it is absent from the nuclei of females. At pachytene a strongly staining sphere (fig. 4b), somewhat smaller than that seen at this stage in males of the birch borer (fig. 4a), is associated with the nucleolus, thus identifying itself as "sex chromatin." In addition, it is associated with two typical pachytene threads which extend from it and become lost among the other euchromatic threads. The sex-complex is therefore composite, consisting

FIG. 8. Poplar borer spermatogonial metaphase: 20 autosomes, a large X and a large but indistinguishable Y chromosome.

FIG. 9. Poplar borer oogonial metaphase: 20 autosomes and 2 large X chromosomes.

FIG. 11. Examples of the XY pair at first metaphase showing the lateral displacement of the heterochromatic portion of the X × 5300.

of both heterochromatin and euchromatin.

At metaphase in primary spermatocytes 10 pairs of elements are present (figs. 10a and b). The paired chromosomes comprising nine of these are equal in size and the pairs usually resemble dumb-bells. The tenth is heteromorphic and is the XY pair. One of its constituent chromosomes, the smaller one or Y, resembles the autosomes in both size and staining capacity. The other, the X, is identical except that it has a less intensely stained body joined to it close to the centromere (fig. 11). In other words, without this lighter-staining, lateral appendage, the XY bivalent would be indistinguishable from the autosomal bivalents. At prometaphase the appendage and the rest of this pair stain with equal intensity, but by full metaphase a marked difference is evident. At the same time, there appears to be a lengthening and narrowing of the appendage, but it is difficult to be certain with such small structures and it might merely be an illusion resulting from the weaker staining reaction. Association between the constituent chromosomes of the autosomal bivalents is presumably always by means of two terminal contact points, and the same is true for the sex pair. All pairs are synchronized in congression.

At anaphase the larger and smaller members of the XY pair invariably pass to opposite poles: disjunction is therefore reductional for the structural inequalities. Consequently, second spermatocyte metaphases are of two types only: one with 10 approximately equal-sized chromosomes, the other with only nine and one definitely larger (fig. 12) and now of conventional appearance. Young spermatids are formed of two types and in equal numbers; one has a strongly heteropycnotic body somewhat smaller than that in birch borer spermatids, the other has none (fig. 13). The former is obviously X-containing, the latter Y-containing.

FIG. 12. Daughter second metaphases in the poplar borer male: 9 + indistinguishable Y and 9 + X.

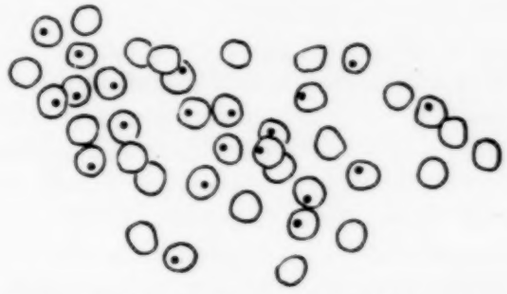


FIG. 13. Poplar borer spermatids: approximately equal numbers with and without heterochromatic bodies × 1540.

DISCUSSION

(a) *The Cytological Differences between the Birch and Poplar Borers*

Males of the birch and poplar borers differ cytologically in a number of ways. First, there is a straightforward numerical difference, the birch borer having 22 individual chromosomes, the poplar only 20. Second, the two sex chromosomes of birch borer males are both smaller than those of poplar borer males, the y of the former being especially minute. Third, the larger X in what we may call the neo-XY system is obviously composite at the first meiotic metaphase, being wholly euchromatic on one side of the centromere but only distally so on the other. Fourth, although the y chromo-

some exhibits negative heteropycnosis at this stage, the Y does not. Fifth, the Xy bivalent is delayed in congression at metaphase; the neo-XY is synchronized with the autosomes. Sixth, though males of both borers form two types of spermatids, with and without heteropycnotic X chromosomes, the heteropycnotic body in birch borer spermatids is clearly larger than that of the poplar borer. On the other hand these forms exhibit a highly significant similarity: both have second spermatocyte metaphase complements of only two types.

(b) *The Method of Origin of the Neo-XY Sex Chromosome Pair*

Numerical differences can arise by either chromosome loss or chromosome "fusion." Actually, in the instance under discussion, both phenomena have contributed to the change: the y as such has been lost and part of the original X is now translocated on to an arm of an autosome in the neo-XY form. The evidence for this conclusion lies in the other differences noted above. The absence of the y is observation; it consists of little more than a centromere, and the number of centromeres has decreased from 22 in the birch to 20 in the poplar form. The second missing centromere is probably that of the original X chromosome. At the origin of the translocation between the autosome and the X, the deletion of one of the two centromeres was obligatory in order to ensure the mechanical stability of the resulting composite chromosome. Though it is immaterial which chromosome suffered the loss, the observational evidence that the one retained is located in euchromatin suggests strongly that the one deleted was from the original X. The relative positions and sizes of the euchromatic and heterochromatic parts of the new X chromosome point to a simple insertion having taken place near the centromere in one arm of the autosome. In the process a large part of the old X became lost from the sex chromosomes, the autosome having apparently suffered no loss in the process. The loss of as much as half of the old X in the origin of the neo-XY complex is compatible with the observed difference in size of the heteropycnotic bodies in the two borers. The unaltered homologue of the autosome involved became, at the moment of translocation, the neo-Y; and the constitution of the two types of males might equally well be formulated at 20A + Xy and 18A + $\widehat{AXA}$, the females as 20A + 2X and 18A + $2\widehat{AX}$ (the yoke over the symbols indicating fusion by translocation). Theoretically, it is because it is largely, if not entirely, genetically active that the neo-Y fails to show heteropycnosis.

At present we have no conclusive evidence why the Xy pair is delayed in congression. But if the delay were conditioned by the extreme size difference of its component members (cf. their coordination with the autosomes when unassociated at second metaphase), the synchronized congression of the neo-XY and the autosomal bivalents in the male of the poplar borer is to be expected.

Finally, their similarity in forming each only two types of second metaphase complements is in complete agreement with the above interpretation. The pairing and differential segments are, relative to each other, in the same positions in both the new and the old sex chromosomes. That there is a distal pairing segment in each arm in the original Xy pair is shown by their meiotic association in the form of a parachute. The lengths of the pairing segments in the X of this system are therefore limited to the minute length of the y arms (fig. 14). Thereby, the lengths and positions of the differential segments in each arm are predetermined. These are both proximal in position and take up most of the length of the X arms. One or both are the seats of the primary sex-determining genes and of any completely sex-linked genes that occur. However, since much of the original X chromosome has been lost in the origin of the new X and the remainder has been in-

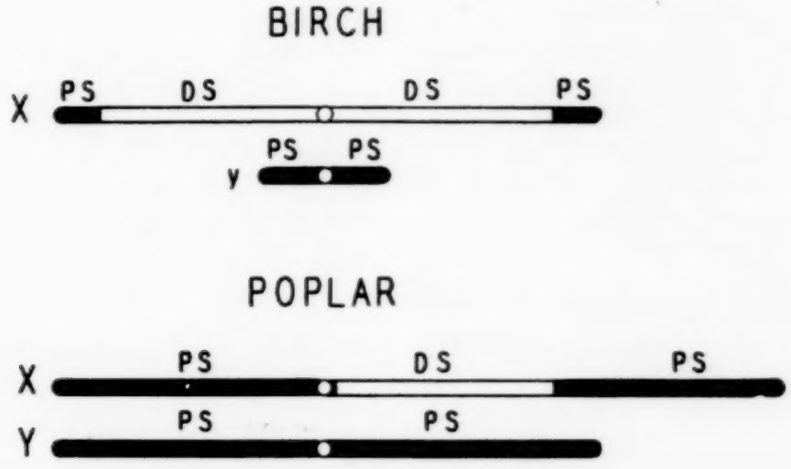


FIG. 14. Diagram showing probable relative sizes and distribution of the pairing (PS) and differential (DS) segments in the birch borer Xy and the poplar borer XY sex-determining systems.

tercalated near the centromere, it would appear that the active sex-determining genes of the original X are restricted in their distribution along that chromosome.

As postulated by Koller and Darlington (1934) and demonstrated by Koller (1941a) a consequence of the centromere being located in the differential segment is that a reductional segregation of structural inequalities at the first anaphase is obligatory; this division, then, is reductional for the sex chromosomes in the male birch borer. In the male poplar borer the first division is likewise reductional. The pairing segments in the XY are again two in number, one in each arm (fig. 14), but, as a result of their autosomal origin, they are no longer small, terminal regions: in the neo-Y they constitute the whole of each arm; in the neo-X, the whole of one arm but only the long distal part of the other. The differential segment does not here include the centromere but is restricted to a proximal position in one arm of the X and has no counterpart in the Y. The restriction to two in the number of types of complements occurring at second metaphase is therefore independent of the number and character of any chiasmata that may be formed in the pairing segments, just as it is evidence that exchanges never occur proximal to the point of intercalation. This we are led to infer also from the uniformity of the first spermatocyte metaphases.

According to Koller (1941b) not only is the cat alone among mammals in possessing an interstitial differential segment but ". . . only in the sex chromosomes of *Phragmatobia* (Lepidoptera) is a similar structure reported by Seiler (1925) . . . ." To these he might have added several, and by inference the majority, of the species of Coleoptera described and illustrated by Stevens as early as 1906. Now, besides the curculionids of Suomalainen (1940, 1947), we may include the borers described herein and a great many others (unpub. data).

The extreme size difference between the X and y in the parachute type of sex chromosomes leaves room in the y for little other than two pairing segments adjacent to the centromere. The fact that the y can be lost without morphological or physiological effect points to its being completely inert. It would appear then that the y is entirely devoid of a differential segment, or, in other words, that the sex-differentiating genes and others completely linked to them may be the sole property of the X chromosome.

(c) *The Sequence of Change from 22 to 20 and from Xy to XY*

The evidence presented here points to the occurrence of two causally related

events in the evolution of the neo-XY from the old Xy system of sex-determination; obviously one must have predated the other in origin. It might be assumed that the birch borer (AA Xy or AA XX) gave rise by translocation, which incidentally necessitates a minimum of three simultaneous breaks and two reunions, to an intermediate type (A $\widehat{AX}$ y) which in turn produced the poplar type ($\widehat{AX}$ A) by the loss of the minute, and then superfluous, y chromosome. The hypothetical intermediate type, with two chromosomes, the y and the neo-Y, subserving the same function, would certainly be mechanically unstable. Three considerations make this postulated method of origin highly probable. First, all of one pairing segment and some, if not all, of the other, upon which the survival of the y is dependent, were presumably lost from the original X at the time the translocation occurred. Second, since the y is partially, if not completely, inert, ordinarily performing a purely mechanical function in disjunction, which is now appropriated by the neo-Y, the y could be readily dispensed with without adversely affecting the viability of the organism. Third, such a mode of origin, involving first translocation, could occur in either the male or the female. The alternative, loss of the y followed by a fortuitous translocation of part of the X on to an autosome, though not impossible, is highly improbable. In origin, it would of course be restricted to the male.

(d) *The Genetic Consequences of the A–X Translocation*

Consequent upon the mode of origin of the neo-XY system and the relative numbers of active genes situated on the original autosome and X chromosome involved, there will, on theoretical grounds, be a sharp increase in the number of genes capable of showing partial sex linkage in the poplar borer relative to the birch borer. Sex linkage will be complete in the differential segment of the neo-X, since there is no comparable region in the Y in which crossing over could occur, but only partial in the pairing segments, if crossing over is free to take place. With this provision, it is probable that there will be increasing sex linkage of genes along both arms with increasing proximity to the point of translocation.

(e) *The Spiralization Relationship of Heterochromatin and Euchromatin*

The unique asymmetry displayed by the neo-XY when paired at metaphase calls for comment. The lateral displacement of the heterochromatic X-portion as a loop proximal to the euchromatic part of the composite X chromosome simulates association by means of a terminalized lateral chiasma (Darlington, 1929, on Tradescantiae). In fact, the peculiarity of the configuration, taken alone, would most readily fit this interpretation; it is, of course, invalidated by the conditions seen to exist at later stages and in gonial metaphases. The appendage-like appearance of the heterochromatic portion might derive from its possession of an independent and earlier spiralization cycle relative to that of the euchromatin (White, 1940a; see also Suomalainen, 1946, on *Phyllodromia germanica*). Such a time differential has been seen to operate in both the Xy and the XY systems (cf. figs. 4a and 4b). In the latter the heterochromatic part of the X is already condensed into a deep-staining sphere while the euchromatic parts are unspiralled, extending from the sphere as two lightly staining threads. Alternatively, the lateral protrusion might result from the original X chromatin being associated with, or perhaps partially embedded in, nucleolar material before the euchromatin starts to condense, as is common with the sex chromosomes of Coleoptera (Stevens, 1906, 1909). In elaterids the nucleolus envelops the sex chromosomes and may in some species persist until the first metaphase (unpub. data). In *Tenebrio*

molitor L., but apparently not in *T. picipes* Hbst., every one of the nine pairs of autosomes shows early procentric condensation in the form of a sharply defined block abruptly separated from progressively more faintly staining distal regions extending out on either side (unpub. data; see also White, 1936, on *Mecostethus*). At metaphase the autosomal bivalents of the two species are indistinguishable; they both show "continuous" spiralization. Thus the latter alternative appears more reasonable, with the nucleolus preventing continuity in spiralization.

(f) *Comparable Changes and the Evolution of Sex-Determining Mechanisms*

The hypothetical intermediate stage beween the birch and poplar borers would, of course, constitute a multiple sex-chromosome system, namely, XYy. But, as we have seen, such a condition would be mechanically unstable and liable to early elimination from the population. On the other hand, it should be stressed that both the Xy and the XY are remarkable in the regularity with which they pair. Among the several hundred nuclei examined not a single example of failure of pairing has been observed in either system. The Xy system, despite the short length of its pairing segments, is therefore perfectly adapted to regular pairing and disjunction. The autosomal bivalents, with their longer pairable length, likewise show complete regularity; and it is presumably this greater length that is the important factor in the efficiency shown by the neo-XY system, upon which a certain handicap would have been imposed following the asymmetry resulting from the insertion of the old X segment. In contrast, Koller (1936) found approximately four, seven, and 13 per cent failure to pair for the sex chromosomes of three marsupials having X and Y chromosomes of a size comparable to those of the birch borer but possessing only one pairing segment. Whereas the complete genotypic adaptation to regular pairing shown by Coleoptera, like the prevalence of the parachute configuration, points to the great antiquity of this type of mechanism, the mechanical instability and the morphological variability in the marsupial system might be regarded as evidence of its recent evolution in that group.

The non-essential y in the hypothetical XYy borer could, of course, become a permanent member of the chromosome complement in two ways. On the one hand, by simple reduplication resulting from non-disjunction, supernumerary chromosomes might be incorporated into the basic set. But in Coleoptera, with regular disjunction presumably dependent on association in the pairing segments, the sizes of which in the y are close to a minimum, there would be a decidedly low limit to their numerical increase (cf. Darlington, 1939b, on Heteroptera). On the other hand, a superfluous centromere bounded by inert material, which the y essentially is, could serve as the focal point for the formation of higher chromosome numbers. Supernumeraries occur in *Diabrotica soror* Lec. and *D. duodecimpunctata* (Fab.) but not in *D. vittata* (Fab.) (Stevens, 1908); and these differ also in that the first two have, in addition to supernumeraries, 18 autosomes and a large X chromosome, and that the third, now *Acalymma vittata* (Fab.), has 20 autosomes and a small X. Whether the smaller X has resulted from the translocation of X chromatin (possibly the original pairing segments) on to a pair of supernumeraries (i.e., old y chromosomes), thus constituting an extra pair of "autosomes," cannot, from Stevens' work, be decided. Were this so, we would have to conclude that in the first place there was a loss of the pairing habit, for the supernumeraries do not pair *inter se*, or with the X in *D. soror* and *D. duodecimpunctata*. Furthermore, we should have proof of the change from heterochromatin to euchromatin following the attainment of the homozygous condition in the heterogametic sex. Be that as it may, the fact

that the only other members of the Galerucinae known cytologically, viz., *Trirhabda canadensis* (Kby.) and *T. virgata* Lec. (Stevens, 1906) and *Galerucella vaccinii* Fab. (unpub.) have an Xy sex chromosome pair, makes the above speculations not implausible. Moreover, it is significant that, although variability in chromosome number is common in the order, the two main families exemplifying the XO system show considerable constancy in the number of their autosomes. And in two cases at least where this fails to hold, the decrease in chromosome number has clearly resulted not from changes involving sex chromosomes but from the "fusion" of non-homologous autosomes (unpub. data on elaterids).

In the course of her pioneer work on sex-determination in the Coleoptera and other orders, Stevens (1906) examined two species of "spruce borers" which were not determined as to genus, as they were collected as pupae. She states, "Most of the spermatocytes contained 10 (pairs of) chromosomes, one of which was plainly an unequal pair. In a few testes the number was 11, indicating that pupae of two species had been collected." Unfortunately, it is not certain from her description that the unequal sex pairs were alike in the two species, but as she does not remark to the contrary it is probable that they were. Since, however, the Xy pair was certainly present in the species with the lower chromosome number, it is apparent that these borers differed not, as in the birch and poplar borers, in the sex chromosomes being Xy in one and neo-XY in the other, but simply in the number of autosomes.

With the exception of changes from XY to XO, the most readily analyzable evolutionary change in sex chromosomes involves "fusion" between an X chromosome and an autosome, that is, a change in the male from an XO to a neo-XY system. This is particularly so if the chromosomes involved are telocentric or almost so (White, 1940b). Reports of such changes in the Coleoptera are confined to three Indian buprestids, *Sternocera nitidicollis* Lap. and Gory, *S. laevigata* Lap. and Gory, and *Julodis whithillii* (Gray) (Asana, Makino, and Niiyama, 1942[4]), although it is not known that the primitive species were XO types. Their evidence, derived in part from a consideration of the heterochromatic and euchromatic constitution of the X and the euchromatic nature of the Y chromosome, is conclusive proof of an origin by translocation involving essentially telocentric elements.

One is led to infer that these authors consider their species to be derived from XO species. Such an assumption is, of course, not necessary. If it were, the neo-XY systems in these beetles would parallel in mode of origin that already firmly established for such Orthoptera as *Hesperotettix* and *Mermiria* (McClung, 1917). On the other hand they may have been derived from species with a more primitive sex-determining mechanism, namely Xy. If so, the y has been dispensed with following the origin of the neo-XY system just as it has in the poplar borer. Further study of Indian relatives of the species in question might conceivably produce evidence on the cytological constitution of their progenitors.

In the lepidopteran *Phragmatobia fuliginosa* (L.), Seiler (1925) has reported the occurrence of three chromosomally distinct races. Ignoring the autosomes, these may be symbolized as XY, XY_1Y_2, and $X_1X_2Y_1Y_2$ in the males. Darlington (1937) has assumed that the XY race is the ancestral one, which gave rise to to the others by successive fragmentation of the Y and X chromosomes. But as White (1940b) points out, the reverse could be equally true. Thus an ancestral AA XY race might by fusion have produced an $AA\widehat{X}XY$ race, which in turn gave rise to the $\widehat{AX}\widehat{AY}$ race. Such a course of evolution, although not an exact parallel, is not very different from what has

[4] I am grateful to Dr. M. J. D. White for calling my attention to this paper.

occurred in the origin of the birch and poplar borers.

Cases of translocation apparently involving sex chromosomes and autosomes are to be inferred in the Heteroptera. In *Rhytidolomia senilis* (Say), a species with a low chromosome number, the heterochromatic X and Y chromosomes have associated with them euchromatic segments which undergo "touch and go" pairing (Schrader, 1940a and b); the latter segments are therefore autosomal in origin. In *Lethocerus americanus* (Leidy) the complement consists of six autosomes and a small XY pair, while a closely related form has only four autosomes and no sex chromosomes, or at least no chromosomes which behave as do typical heteropteran sex chromosomes (Chickering, 1932; Chickering and Bacorn, 1933). Chickering and Bacorn consider that the sex chromosomes have been translocated into an autosomal pair, and that the two remaining pairs, seen in *L. americanus*, have fused into one. White (1945) points out, "The only possible alternative to this interpretation would be that the X and Y had really been lost from the chromosome set, the function of sex determination having been taken over by one of the autosomes." It is, however, also possible that, as in the poplar borer, only the Y has been lost, the X having been totally or partially incorporated in an autosome.

The occurrence among the XY beetles of perhaps no more than eight species known to be characterized by the possession of a sex pair in which both chromosomes are large, points to their derivation from Xy species by translocation between autosomes and sex chromosomes. Except in the Indian borers already discussed, this possibility is considerably strengthened by the fact that five of these species are unique also in the lowness of their chromosome numbers. Thus, *Oryctes nasicornis* (L.) (Prowazek, 1902), *Phanaeus igneus* MacL., *Ph. vindex* MacL. [= *Ph. carnifex* (L.)] (Hayden, 1925), and *Cleis hudsonica* each have $2n = 12$, and *Arthromacra aenea* has $2n = 14$. The lowest number known to me among the Xy species is *Chalepus dorsalis* [= *Odontota dorsalis*] (Stevens, 1906) with $2n = 16$, although a lower number, $2n = 11$, occurs in the XO weevil, *Sitophilus oryzae* (L.) [= *Calandra oryzae*] (Gunson, 1945). Whether the large XY condition in these five species arose by translocation remains to be investigated. At the moment and in the absence of information as to the conditions in the progenitors of the Indian buprestids it appears that the dual change, X-autosome translocation and loss of the y chromosome, described herein is unique and as such constitutes an addition to our knowledge of the mechanisms involved in chromosome evolution.[5]

From an extensive survey of the saltatorian Orthoptera, White (1941) has been led to formulate the "Principle of the Structural Isolation of the X." He finds that evolutionary changes in the sex chromosome in that order (XO for males) are confined almost exclusively to segmental rearrangements within the X chromosome. With the exception of "whole arm transfers," that is, fusions between the acrocentric X and acrocentric autosomes, no interchange of chromatin occurs beween them. In *Agrilus anxius* auct. we see a rather striking exception to this principle, but the extension of White's principle to the Coleoptera in general seems

[5] Since this paper was written, Dr. W. J. Boyes of McGill University has shown me a photograph of the first spermatocyte chromosomes in *Tribolium confusum* Duv. It was surprising to see a large XY complex and only eight pairs of autosomes, as my experience with tenebrionids had led me to expect nine pairs of autosomes and a large X-small y sex complex. It was particularly gratifying, therefore, to find this expected complement in the closely related *Tribolium castaneum* (Hbst.), showing that *T. confusum* constitutes a second example of X-autosome translocation and loss of the Y. I have confirmed Dr. Boyes' findings by the examination of *T. confusum* from a distinct source, and other species are currently under investigation. It is hoped that this work will be published in the near future.

highly probable from the results of investigations now in hand.

Acknowledgment

I wish to express my appreciation to Professor Franz Schrader and Professor C. Leonard Huskins for critically reading the manuscript.

Summary

Two buprestids, species A on poplar and species B on birch, currently referred to the species *Agrilus anxius,* differ in chromosome number and sex chromosome type. Species B conforms to the formula 20A + Xy (minute Y chromosome); species A is 18A + XY (large Y chromosome). Males of both show heteropycnosis, usually positive and associated with the nucleolus but negative at metaphase I. The heteropycnotic element is larger in B. The sex pair in both is associated at metaphase I by two terminal contact points; Xy then resembles a parachute, is late in congression, and is wholly negatively heterochromatic; XY resembles the autosomes in congression time and, except for a pale, lateral protrusion near the centromere of the X, in staining capacity. Anaphase I is reductional for the structural inequalities of the sex pair in both species.

The differences between A and B result from chromatin loss and translocation: the inert y as such has been lost and an acentric part of the X intercalated into an autosome near its centromere in the A species. The neo-Y and its homologous regions in the neo-X remain euchromatic, the original X portion remains heterochromatic; hence the size difference in the heteropycnotic bodies. The lateral displacement of the heterochromatin in the neo-X at first metaphase derives from either a differential spiralization cycle or, more probably, its prophase association with the nucleolus. The pairing and differential segments are respectively distal and proximal in both systems; hence the prereduction. Alternative formulae are therefore: 20A + Xy for B ♂♂ and 18A + $\widehat{AX}$A for A ♂♂.

Of the 100 odd Coleoptera known cytologically, about 65 are Xy and only about eight XY. This fact and other evidence point to the following mode of origin: 10AA + Xy → 9AA + A$\widehat{AX}$y → 9AA + $\widehat{AX}$A. The A species is therefore derivative.

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SOURCES OF GENETIC VARIATION IN *PARTHENIUM ARGENTATUM* GRAY (COMPOSITAE)

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The following study is concerned with certain aspects of the part played by sexuality, apomixis, polyploidy, and interspecific hybridization, in producing the diversity of variants found in the *guayule rubber plant*. These major processes operate singly and in combination to produce an extremely complex evolutionary pattern for the species. Their role in this is approached through experimental studies of a population in a uniform environment and by studies of wild populations in Mexico and Texas. The amount and area of occurrence of introgression from the related *Parthenium incanum* is emphasized. The effects of introgression on polyploid facultatively apomictic populations are shown. The whole study has been made from populations and materials ordinarily regarded as belonging to the species *Parthenium argentatum*.

If environmental influences are excluded, the sources of variation within biological groups, from a breeding population to the species as a whole, are basically genetic. Certain genetic mechanisms produce heterogeneity. Others segregate the heterogeneous components of a population, thus providing variants for possible establishment as recognizable taxonomic entities. The actual emergence of new free living types is dependent upon still other factors which affect the stabilization and establishment of the variants once they are segregated. These factors need not be genetic, but may be any type of barrier or major deterrent to the free interchange of genes between the segregant and the population from which it arose. The evolutionary fate of a variant thus produced is subject to a whole spectrum of possibilities. In general, the methods of genetics are not usable to determine what actually becomes of such a variant evolutionally. With appropriate data and their statistical treatment, predictions as to the probabilities of survival, or the chances of a given type becoming dominant, may be made. But it remains largely for the paleobotanist and comparative morphologist to chart the actual course of a given evolutionary sequence. Experimental methods of attack on such problems are limited principally by the time factor in nature which cannot be duplicated or predicted. However, experimental procedures may be effectively employed to show how natural evolutionary events most probably took place in many instances. Both experimental and comparative methods have been used individually and in combination to elucidate the facts concerning *Parthenium argentatum* which follow. In this species, there is a combination of characteristics which establishes its area of origin and permits revealing studies on several factors important in its evolution. Though the species has been worked with in some detail, much remains to be done. Most of the needed data must come from future field studies in Mexico.

EVIDENCE OF HETEROGENEITY

In studying the variation found in guayule, it is necessary to make allowances for certain phenomena not characteristic of a diploid sexually reproducing species. To begin with, a polyploid chromosome series of $2n = 36+$, $54\pm$, $72\pm$, $90\pm$ and $108\pm$ is present (Stebbins and Kodani, 1944; Bergner, 1946). So far, the $36+$ chromosome plants have been found to be sexual and those above that level facultatively apomictic (Powers and Rollins, 1945; Esau, 1946). Studies of certain populations have amply demonstrated that a portion of the variability found is

attributable to introgressive hybridization with the related species, *Parthenium incanum* (Powers and Rollins, l.c.; Rollins, 1944, 1945). In order to present a clear picture of the scope and magnitude of heterogeneity for the species as a whole, it has been necessary to treat separately the chromosomal, sexual and facultatively apomictic groups, and those showing introgression from *P. incanum*.

The data summarized in table I were taken on plants grown in replicated experiments in a uniform environment at Salinas, California. Details of seed sources, design of experiments, and handling of plants, are given by Bergner (1946) and by Kramer (1946). It is evident from the data presented that there is considerable variation in both morphological and physiological characteristics of the plants of different populations from the same geographic area. This is equally true whether facultatively apomictic or sexual populations are considered. In all characteristics except plant height, the two populations showing introgression from *P. incanum* digressed more than any of the others from the pattern shown in all populations studied. This was to be expected. However, it is clear, from a study of the data presented concerning the five Durango populations, that variation independent of introgression from *P. incanum* is considerable. These populations were wholly sexual and the variation indicated was due to ordinary genetic segregation. Environmental effects were equalized by the design of the experiment. The increase in lateness of flowering shown by the three 54 ± chromosome Durango populations over the five 36 + chromosome populations from the same area, is undoubtedly associated with the increase in chromosome number. Presumably, the same association holds for the Texas populations as compared to those

TABLE I. *Heterogeneity in Parthenium argentatum* [1]

Category examined	Range or mean	Plant height in cms. (1944)	Leaf-length in cms. (active stage)	Number of leaf-points (active stage)	Days to over 50% flowering after April 1, 1945	Rubber, per cent
36 + *Chromosome sexual*	High	42.01±0.605	8.90±0.186	2.17±0.118	8.4±0.88	5.27±0.101
5 populations	Low	37.87±0.552	7.92±0.178	1.46±0.134	3.8±0.29	4.74±0.133
(Durango, Mexico)	Mean	38.98±0.303	- - - - -	- - - - -	- - - - -	4.94±0.116
54 ± *Chromosome apomictic*	High	41.94±0.867	9.37±0.187	2.75±0.092	17.1±1.17	6.54±0.143
3 populations	Low	35.86±0.612	8.34±0.162	1.79±0.060	8.3±1.29	4.45±0.126
(Durango, Mexico)	Mean	38.72±0.417	- - - - -	- - - - -	- - - - -	5.70±0.611
72 ± *Chromosome apomictic*	High	33.55±0.525	8.54±0.131	2.94±0.066	18.7±1.27	5.93±0.125
16 populations	Low	30.72±1.237	8.13±0.090	2.48±0.063	15.3±0.47	5.06±0.173
(Southern transpecos, Texas)	Mean	32.32±0.157	- - - - -	- - - - -	- - - - -	5.42±0.068
14 populations	High	34.04±0.414	8.50±0.129	2.43±0.105	30.8±0.89	6.20±0.110
(Northern transpecos,	Low	30.44±0.862	7.65±0.114	2.08±0.054	15.2±0.93	5.21±0.090
Texas)	Mean	32.54±0.139	- - - - -	- - - - -	- - - - -	5.71±0.085
2 populations showing	High	38.58±0.671	6.92±0.155	4.68±0.094	24.1±0.94	4.83±0.088
introgression from *P.*	Low	36.11±1.021	6.72±0.115	4.18±0.136	20.7±1.22	4.16±0.088
incanum (Texas)	Mean	37.34±0.601	- - - - -	- - - - -	- - - - -	4.50±0.400
All populations studied	High	42.01±0.605	9.37±0.187	4.68±0.094	30.8±0.89	6.54±0.143
	Low	30.44±0.862	6.72±0.115	1.46±0.134	3.8±0.29	4.16±0.088

[1] A portion of the data here presented was assembled and treated by members of the Genetic Division of the Guayule Research Project, U. S. Dept. of Agriculture, Salinas, California.

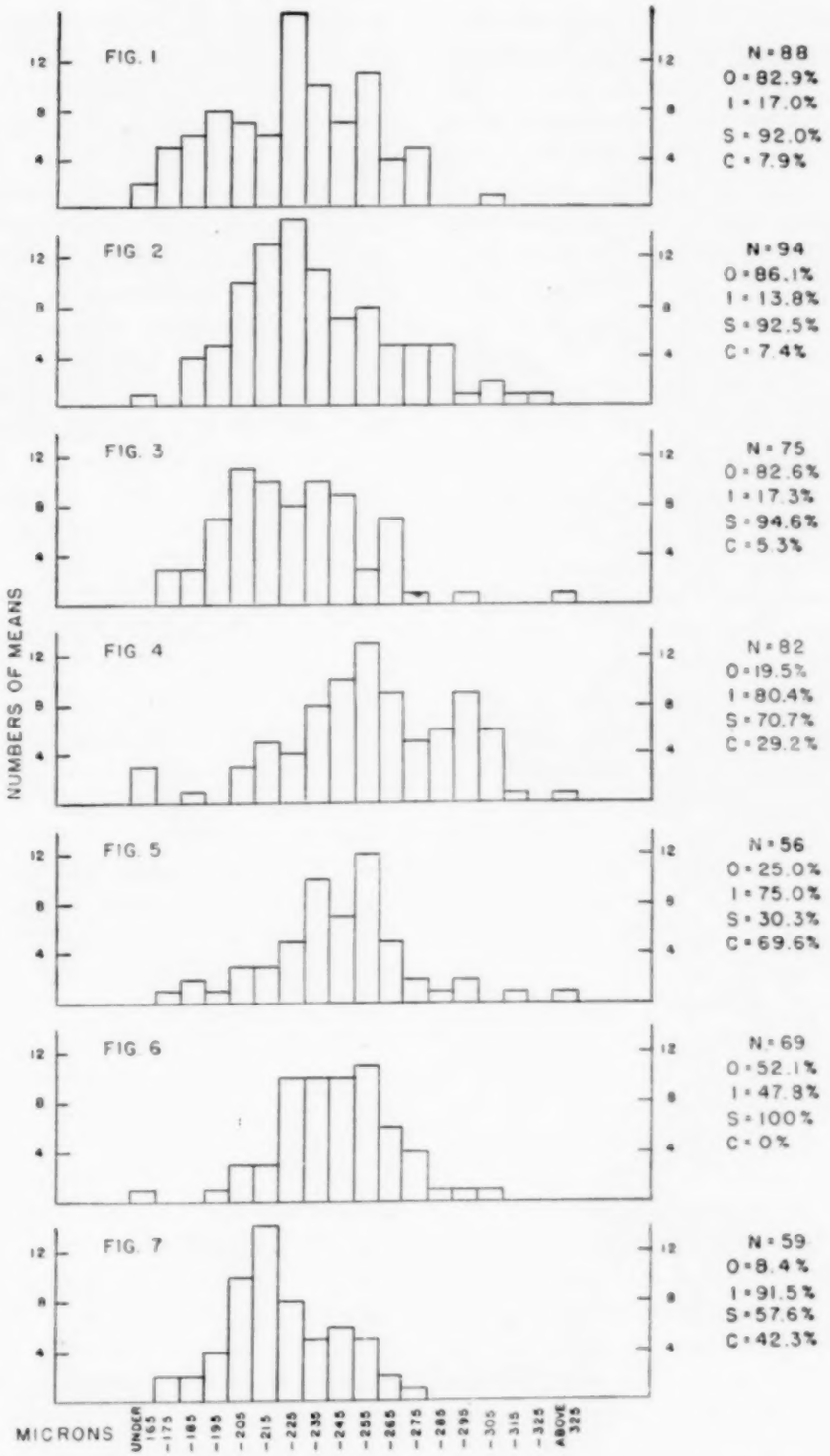
from Durango, but here it should be observed that lateness may also be associated with a more northerly latitude of origin. An interesting geographic trend is seen in the data on the number of leaf-points present. Those populations from the State of Durango have the lowest number of leaf-points, and those northeastward toward the periphery of the species range have the highest, excepting the populations showing interspecific introgression, which have the highest of all. This geographic trend appears to reflect upon the purity of the species outside the Durango region and is touched upon again in considering the area of origin for the species.

A single population occupying an area about 15 miles wide by 20 miles long, on the 02 Ranch, 53 miles south of Alpine, Texas, was thoroughly sampled by LeRoy Powers and W. T. Federer in 1942. The experimental populations produced from the seed gathered were studied by Kramer (l.c.), who presented data concerning plant height, plant spread, percentage of rubber and resin, and days from April 1 to first bloom. As might be expected, the magnitude of heterogeneity in this very thoroughly studied wild population was not as great as that indicated in table I for the species as a whole. For example, the range in plant height for 23 accessions of straight *P. argentatum* was 30.0 to 33.4 centimeters. In 19 accessions showing introgression from *P. incanum*, the range was 31.4 to 35.9 cms. The range for plant height in this whole population was 30.0 to 35.9 cms., as compared to 30.4 to 42.0 for all accessions summarized in table I. An accession of *P. incanum* from the same location showed an average height of 66.6 ± 1.2. Considering the fact that the 02 Ranch population was uniformly of the 72 ± chromosome group and all accessions showed facultative apomixis, the amount of heterogeneity present was rather large. However, the general picture of variability is similar to that found for the percentage of aborted pollen grains by Powers and Gardner (1945). In this characteristic, the means for all locations ranged from 16 to 40%, while the greatest range within one location was from 16 to 22% of aborted grains. In these studies, it was shown that both genetic heterogeneity and heterozygosity were factors in producing the variability found in the 36 + chromosome sexual type, but only heterogeneity was demonstrated to be involved in producing the variability found in the facultatively apomictic group.

Introgression from *P. incanum*

In most characteristics, it may readily be seen that introgression from *P. incanum* extends the heterogeneity rather markedly beyond that found in populations lacking it. Crosses between *P. argentatum* and *P. incanum*, and subsequent backcrosses of the F_1 to *P. argentatum* (Rollins, 1945), have demonstrated patterns of morphological modifications in the resulting progenies. The modifications thus produced in the numerous trichomes of the leaf-surfaces lend themselves to quantitative as well as qualitative studies. The trichomes are lengthened, become more crooked, and the point of attachment becomes more acentric with increased influence from *P. incanum*. Using the trichomes from specimens of over 50 plants taken at random from each of seven populations of *P. argentatum*, in Coahuila and Zacatecas, a study has been made of the nature and extent of introgression from *P. incanum*.[2] Ten trichomes from each sample were measured and each sample scored as to whether the trichomes were predominantly straight (S), or crooked (C), and whether they were predominantly attached at or near the mid-point (0), or between the mid-point and one end (1). The results of the measurements in microns of the cap cell are shown in figures 1–7, in which the means for trichome length for each sample are used in producing the graphs. Near the graphs at right are shown the data on the trichome classifications.

[2] The sampling was done by Dr. W. A. Campbell, to whom my appreciation is here expressed.



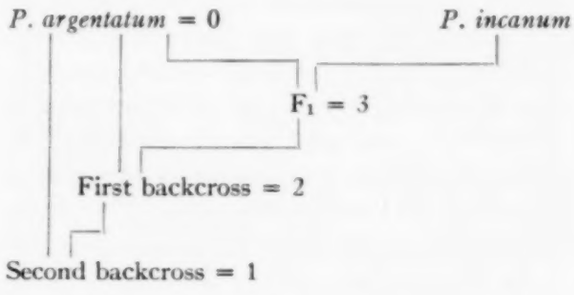
FIGS. 1–7. Frequency distributions of means for the length of ten measured trichomes of samples of plants taken at random from wild populations. The number of samples (N) used is given to the right of each figure. See text for explanation of 0, 1, S, and C. Location of populations, Mexico: Fig. 1. Mts. east of Rancho San José, Coahuila; Fig. 2. Mts. of Rancho San José; Fig. 3. Mts. southeast of Rancho San José; Fig. 4. 6 miles west of Saltillo, Coahuila; Fig. 5. between Comacho and Cedros, Zacatecas; Fig. 6. near Cedros, Zacatecas; Fig. 7. about half-way between Adios and Comacho, Zacatecas.

Unfortunately, from the point of view of studying the whole species, the localities of the populations sampled are not widespread. Those of Coahuila are all in the southeastern corner of the State and those from Zacatecas are in the northeastern portion of that State, none of them over 100 miles from the Coahuila locations. All are from an area where introgression is widespread. The data from three populations in the vicinity of Rancho San José (figs. 1–3) are in close agreement and indicate that these local populations are probably parts of a much larger disrupted population with similar characteristics throughout. Gene transmission within the larger population must be relatively easy and frequent. No plants of *P. incanum* were seen in the immediate vicinity of the Rancho San José populations studied; yet the marks of introgression from that species were unmistakably present. Similarly, *P. incanum* was not seen near the population 6 miles west of Saltillo (fig. 4), but the effects of introgression are strikingly shown by the data obtained. Over 80% of the plants studied showed the trichome attachment to be very acentric, and in over 70% the trichomes were crooked. The frequency distribution of trichome-lengths shows a definite swing to the longer classes in figure 4, as compared to figures 1–3, a further indication of introgression. There is a statistical bimodality in the frequency distribution of figure 4, showing that genes affecting trichome lengths are in two groups in the population. Presumably, those from *P. incanum* have not penetrated the entire population structure. That other genes involved in the introgression from *P. incanum* are similarly disposed in the population, is shown by the classification of the samples shown in table 2. Here, a definite gap is shown between the samples classified as straight guayule and those comparable to an intermediate F_2 of a backcross to the recurrent *P. argentatum* parent.

Of the three Zacatecas populations studied, the one between Adios and Comacho, on the basis of trichome-length, showed the least introgression (fig. 7), although a high percentage of the trichomes were acentric as to the point of attachment. None of these populations showed the neat correlations between trichome-length and the other characters scored, as did those from Coahuila. In the Zacatecas locations, *P. incanum* was intermixed or nearby, while being absent from the Coahuila localities. In the San José area, evidently somewhat of an equilibrium had been reached and the introgressive effects from *P. incanum* appeared to have become stabilized. This is reflected in the data presented, and is in accord with the principle set forth by Anderson (1939) that "variation between individuals will lessen as parental character combinations are approached." One surmises that the initial crosses of *P. argentatum* with *P. incanum* took place at some distance from the present populations and at an early enough period for the effects to have become largely assimilated. In contrast, in the Zacatecas populations studied, penetrations of *P. incanum* genes were probably actively taking place. The introgressions of different genes and gene combinations were apparently proceeding at different rates. Affected characteristics showed varying amounts of introgression from *P. incanum*. Thus, in the Cedros population (fig. 6), the trichomes were nearly all straight, indicating little penetration had taken place. At the same time, almost half of them were acentrically attached, indicating somewhat greater influence from *P. incanum*. The length of the trichomes also indicated a moderate amount of introgression. A similar lack of correlation exists in the Comacho-Cedros population (fig. 5).

The samples from six of the seven populations given above were scored from over-all observations as to the amount of introgression indicated. The scoring was done on a comparative basis, using specimens of known origin for standards of comparison. Thus, the F_1 of a *P. argentatum* × *P. incanum* cross was assigned

No. 3; the F_2 of the first backcross to guayule, No. 2; the F_3 of the second backcross, No. 1; and straight guayule, 0, according to the following scheme:



The F_2 and F_3 plants used for comparison were selected to represent the most frequent type found in the progeny. The F_2 plants were roughly intermediate between the F_1 and *P. argentatum*, the F_3 plants were intermediate between the F_2 and *P. argentatum*.

The wild plants were compared to these known types and rated accordingly using the appropriate symbols. The principal points governing the rating were (a) ratio of width to length of leaf, (b) number of teeth on the leaf, (c) bluntness or sharpness of the teeth, (d) shape of the leaf apex, and (e) nature of the pubescence—whether closely appressed or loosely arranged. Plants of unadulterated *P. argentatum* tend to have narrow, elongate leaves, with an acute apex and with one or two sharp teeth or none at all. The pubescence is closely appressed. In contrast, the leaves of *P. incanum* are shorter and much broader with a shorter petiole, few to several blunt lobes, a blunt apex, and a very loosely arranged pubescence. In table 2, group 0 shows no dectectable introgression from *P. incanum*, group 1 shows a small amount of introgression, group 2 a greater amount, and group 3 is roughly intermediate between the two species.

The data of this table show that five of the six populations sampled are either pure *P. argentatum* or show only slight introgression (Groups 0 and 1). However, all populations show evidence of introgression from *P. incanum*. The population 6 miles west of Saltillo has two separable groups. The samples falling into Group 2 show many evident characteristics traceable to *P. incanum*. Whether these two groups are being partially maintained as separable entities, possibly through apomixis, or are in the process of becoming a continuously variable population, cannot be determined from the data taken. Judged by the relatively continuous variations found in the other populations which are also subject to facultative apo-

TABLE 2. *Estimate of introgression in six populations*

	Number of Samples	Group 0 %	Group 1 %	Group 2 %	Group 3 %
(Fig. 2) Mts. of Rancho San José	94	51.06	36.17	10.60	2.12
(Fig. 3) Mts. southeast of Rancho San José	75	50.66	36.00	10.66	2 66
(Fig. 4) 6 mi. west of Saltillo	82	53.65		46.34	
(Fig. 5) Comacho-Cedros	69	23.21	62.50	14.29	
(Fig. 6) near Cedros	56	59.42	40.57		
(Fig. 7) Adios-Comacho	59	42.37	57.62		

mixis, the two entities now present would be expected to disappear gradually. It should be noted that the habitat in which the greatest amount of introgression was found did not differ conspicuously from that of the other populations studied. None of the habitats were markedly disturbed by man, although the shrub had been harvested for rubber production in previous years.

Geographic Distribution of Pure Types and Types Showing Introgression

All of the living collections and specimens available have been classified by studying them comparatively with pure *P. argentatum*, artificially produced hybrids with *P. incanum*, and various backcrosses. By using the scheme described above, with No. 3 for the F_1, No. 2 for the first backcross, No. 1 for the second backcross, and 0 for pure *P. argentatum*, the approximate amount of introgression present was indicated. It should be clearly understood that the specimens or plants classified in any given group are not genetically equivalent. The classification is an attempt to indicate the approximate level of introgression from *P. incanum* by using known types as standards of comparison.

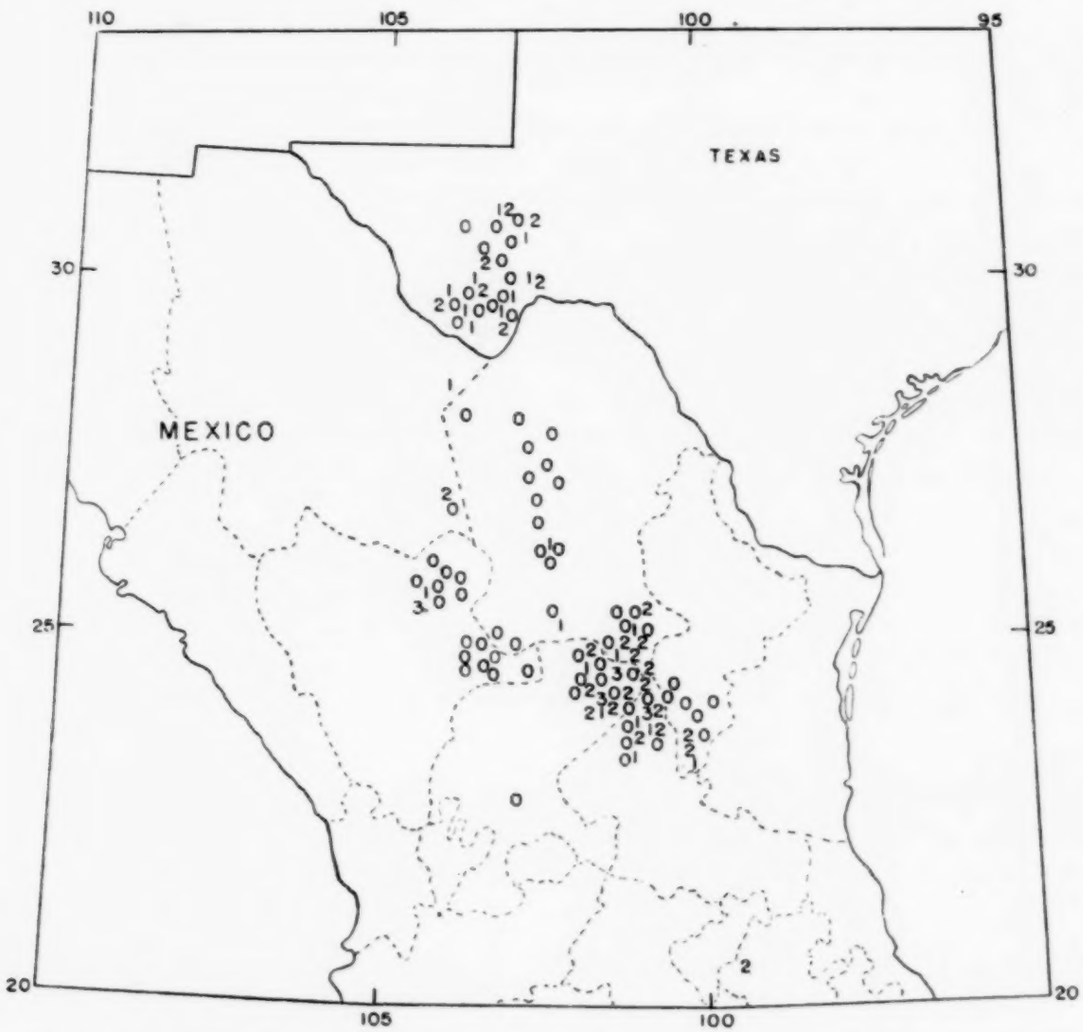


Fig. 8. Geographic distribution of *P. argentatum* showing locations where the pure species and introgressed types have been found. 0 = pure *P. argentatum*; 3 = equivalent of F_1 between *P. argentatum* and *P. incanum*; 2 = equivalent of F_2 from F_1 backcrossed to *P. argentatum*; 1 = equivalent of F_3 from intermediate F_2 backcrossed to *P. argentatum*.

The data obtained were plotted on a map and are shown in figure 8. From this evidence, it appears that *P. argentatum* is purest in the middle portion of its geographic range, and introgression is most common northeastward in Texas and southeastward in the area where the States of Coahuila, Nuevo Leon, San Luis Potosi, and Zacatecas adjoin. It is in the area of least introgression in northeastern Durango where the sexual low chromosome plants of *P. argentatum* have been found. These plants, with s.n. = 36 + chromosomes, presumably predominate in the area. When manipulated experimentally, they cross readily with *P. incanum* which is also found there, but hybrids apparently occur only rarely under natural conditions. Thus it appears somewhat paradoxical that where the sexually reproducing types are found, and one might expect interspecific crosses to occur freely, resulting in swarms of hybrids, this is not the case. Contrariwise, in areas where apomixis is predominant and one might expect little or no interspecific crossing, it is of fairly frequent occurrence with the hybrids persisting.

From experience in the experimental plots, one immediately surmises that the usual expectation is upset by the effects of polyploidy. Previous evidence (Rollins, 1946) showed that polyploidy permitted wide interspecific crosses otherwise impossible, and that the fertility of such hybrids exceeded that of hybrids produced on the diploid level. Thus in the Durango area where the diploid (Bergner, 1946) sexual phase of the species abounds, interspecific hybridization, when it does occur, is less effective in producing persistent new biotypes or introgressed populations than elsewhere in the range of the species. Apomixis does not prevent interspecific crossing because it is not obligate, there being always a certain percentage of fertilized seeds produced by members of a given population. The prevailing type of apomixis present involves agamospermy, apospory, and pseudogamy. Usually when fertilization replaces pseudogamy, an unreduced egg is fertilized, but not always. Sometimes the egg has the reduced number of chromosomes. Complex results are obtained with these alternatives operative, both within the species *P. argentatum* and in interspecific crosses (Rollins, 1945). For the present purpose, it appears necessary only to demonstrate that polyploidy facilitates the initial crosses between the species on a basis that allows the progeny to survive in competition with parental types. The first prerequisite is seed viability. Unfortunately, data from appropriate crosses between *P. argentatum* and *P. incanum* are not available. However, inferences may be drawn from two crosses, *P. argentatum* × *P. hysterophorus* and *P. argentatum* × *P. stramonium* (Rollins, 1946). In the former, *P. hysterophorus* could not be successfully crossed with diploid *P. argentatum,* even though many reciprocal pollinations were made. But, when polyploid *P. argentatum* was pollinated from *P. hysterophorus,* some viable seeds were produced. The resulting hybrids were vigorous but possessed a low fertility.

In another case, summarized data from 15 plants of two separate crosses of diploid *P. argentatum* × *P. stramonium* showed a mean percentage of 4.8 ± 0.444 viable seeds. In four similar crosses where polyploid *P. argentatum* was used, the mean for 36 plants analyzed was $13.0 \pm 0.480\%$ viable seeds. These two cases clearly demonstrate that polyploidy does facilitate interspecific crossing in *Parthenium,* at least outside the *P. argentatum* –*P. incanum* combination, and in the latter the geographic correlation of polyploidy and introgression points to the same thing in these species.

As to the ultimate survival of the segregates produced in the above indicated ways, it may be pointed out that such types are widely distributed geographically and in many instances are thoroughly established as populations and races of the species as a whole. It is clear that these types showing introgression from *P. incanum* are not only wide-spread in space,

but have arisen at different times, perhaps over a very long period. Some are sufficiently successful to have become the dominant type in the area where they grow. One semi-isolated population, extending over more than forty square miles of area (near Sanderson, Texas), is composed entirely of plants showing introgression from *P. incanum*.

Discussion

It has been commonly assumed that apomixis, due to its isolating tendency, does not affect in a major way the actual origination of new biological types. Insofar as it operates strictly as an isolating mechanism, this is undoubtedly true. But where apomixis is only facultative, gene flow through a population is permitted. The effect should be, in part, that of slowing down the transmission of genes from one portion of a population to another, or the introgression of the genes of one species into another. This slowing process would tend to accentuate the usual effects of linkage and may provide a crucial advantage in the production of recognizable variants over cases where only linkage is operative. In the usual sexually reproducing population, gene combinations favorable to survival are transient. Without doubt the vast majority of potential variants in such a population fail to overcome competition or to meet with the favorable environmental factors necessary for survival and perpetuation. Theoretically, facultative apomixis would provide more time, in terms of plant generations, for a given gene combination to become established. For example, an introgressed plant with favorable growth characteristics but with a high percentage of infertility might survive for a period of time by reproducing apomictically, whereas in a sexually reproducing population it would be immediately lost. Also, favorable gene combinations could be preserved for a time from segregation. Thus apomixis might provide opportunities for such a plant to increase its fertility or to contribute to some other favorable combination.

The commonly recognized association of apomixis and polyploidy (Gustafsson, 1947) is present in *P. argentatum*. It seems clear that the higher chromosome types more readily produce persisting interspecific hybrids and backcrosses than the diploid phase of the species. Apomixis and polyploidy combine to add many complications to the pattern of introgression of *P. incanum* into *P. argentatum*. The effects of introgression upon the latter species almost throughout its present geographic range are striking indeed. But in some of the local populations studied, the evidence of introgression indicated a pattern of genic penetration not unlike that expected in introgressing diploid species (Anderson, 1949). The curve for variability in at least four separated populations was that of a normally sexual interbreeding and introgressing population showing considerable linkage. Yet facultative apomixis and polyploidy were known to be present in all four cases. This seemed remarkable in view of the potential strength of apomixis as an isolating mechanism. In these instances, genes of *P. incanum* had become introgressed and were thoroughly enmeshed in the pattern of variation of the populations. One expects the effects of polyploidy and facultative apomixis in either producing or accentuating variation to be in a sense additive to the variation found in the diploid sexually reproducing phase of the species. This appears to be the case in *P. argentatum* viewed as a species. But in given local populations additive effects are not always detected. More data from a wider sampling of the species are needed to determine whether this difference is real or only seemingly so.

Considering only the populations which did not show introgression from *P. incanum*, it was equally unexpected to find the range of variation in the facultatively apomictic populations to be nearly as great as the variation in the sexually re-

producing ones. Presumably segregation in the latter was uninhibited except by such mechanisms as linkage, and considerable heterogeneity was actually found. It was unexpected to find the rather large amount of heterogeneity in the facultatively apomictic populations. Here, one might have expected apomixis to have had a restrictive effect on segregation resulting in more uniform populations. However, it appears that sufficient segregation is permitted by the infrequent sexual process in the production of seeds to keep these populations nearly as heterogeneous as those where sexuality is the only type of reproduction known.

In most species of plants, it is difficult if not impossible to locate precisely the area where the species originated. It would often be useful to know this, since evolutionary trends within the species and distributional patterns could then be arranged in their proper geographical sequence. In *P. argentatum,* there are fairly strong indications that the area of origin is eastern Durango, or in that general region. Here, the diploid phase of the species is found, whereas polyploids are predominant elsewhere in the species-range. Also, the sexual phase of the species is found chiefly in eastern Durango, while facultatively apomictic types are most abundant elsewhere. Diploidy must have preceded polyploidy, and sexuality undoubtedly preceded apomixis. Therefore, the area where the diploid sexual phase of the species occurs, i.e., eastern Durango, was undoubtedly occupied by *P. argentatum* prior to its spread northward and in a southeasterly direction. Being first occupied and still supporting the least adulterated portion of the species, the Durango area becomes the logical choice as the area of origin for the species.

Summary

The heterogeneity found in *Parthenium argentatum* is traceable to several sources. The always important segregation of genetic materials within the species is certainly operative, as indicated by the variation found in diploid sexually reproducing populations of the species. This is undoubtedly fed in part by mutations but no attempt to analyze the role of mutations in this respect has been made in the present study. Our survey of heterogeneity shows the range of variation to be fairly wide even in that portion of the species which is unadulterated by *P. incanum.* As expected, the range of variation is much greater when the whole geographic area of the species is considered than it is in a given local population. Morphological and physiological characteristics show relatively similar magnitudes of variation.

Introgression from *P. incanum* has played a major role in extending the heterogeneity much beyond the limits otherwise to be expected within *P. argentatum.* It has been a major source of different genetic materials which have been variously incorporated into new and otherwise unexpected combinations. Thus, a very wide range of variation characterizes the evolutionary pattern for the species, *P. argentatum.* Introgression is more prevalent in polyploid facultatively apomictic populations than in diploid sexual ones.

Apomixis in *P. argentatum* is facultative, permitting gene-flow in the species and in local populations. Yet seed-fertile segregates of interspecific crosses are partially protected from the swamping effects of a freely interbreeding population and are aided in becoming established where no other known isolating mechanisms are operative. Ecological preferences or barriers appear to have had slight influence on the establishment of variants in the populations studied.

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THE SPECIES CONCEPT: A DISCUSSION

THE SPECIES CONCEPT: A SEMANTIC REVIEW

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In some respects, it is extremely unfortunate that names are ever attached either to ideas or objects. The false attachment of names to ideas or objects similar but not identical with the original can work harm far exceeding the benefits conferred by having a convenient label. The name "species" has come to such a state.

As we shall see, a species, be it plant or animal, is a fiction, a mental construct without objective existence. Animal, and plant, lines of descent exist in a four-dimensional continuum. To set up species in this continuous line of descent, we must chop it into units, and in any such process the divisions are purely arbitrary. Available information makes such a view more or less self-evident. What, then, is a "species"? Instead of starting with an evolutionary line and dealing with it on the basis of preconceived concepts, working from the top down, so to speak, let us work from the bottom up.

Our starting point will be an individual animal, which for convenience we will say answers to the name of John. John is a sexually-reproducing animal. As such, he comes into existence at the moment that certain sperm and egg nuclei fuse, at which moment we may refer to him as $John_0$, one cell with a nucleus. The next time we look for $John_0$, we can't find him. In his place, we find a stranger with two cells. Ah-ha, we say, John has undergone cell-division. We are confident that if we had observed $John_0$ we would have seen his continuous transformation into this two-celled stranger who is obviously *not* $John_0$. Since we are sure he does have some sort of a very close relation to $John_0$, we decide to call this new animal $John_1$. Similarly we find $John_1$ displaced by $John_2$ and he by $John_{3, 4, 5, \ldots n}$. Thus we have followed what is usually called the "growing-up," or the ontogeny of an individual. But *what* is John? Obviously, he is not the same thing at any two successive instants. Now he is $John_{1324}$; the next instant he is $John_{1325}$, forever and irrevocably different from any John that has come before or from any that will come in the future. Thus John is a succession of conformations of matter in time, and any meaningful study of him will have to consider the four-dimensional $John_{0+1+2+3+4+ \ldots n}$.

One fine spring day the tender passion stirs $John_n$'s breast, and he looks around for a mate. Within his immediate horizon he espies $Jane_{n+1}$, $Joan_{n+2}$ and $June_{n+3}$. For reasons too devious to explore at this time, $John_{n+4}$ chooses $Jane_{n+5}$ for his mate, or perhaps, *vice-versa*. Thus we pass from the individual to the breeding population, our next meaningful unit.

What precisely is a breeding population? From John's point of view, it includes all females with whom he might ordinarily mate; in other words, it takes in a territory extending from a central point out to the limits of John's wanderings. Such a territory includes males who would be equally glad to mate with the females of this same area. The total population of males and females ready, willing, and able to interbreed and centered around a particular animal we may denote a breeding population. Each individual in this population will also be the center of another breeding population, most of which will have territories extending beyond the original one. The character of a given breeding population is never identical at any two moments.

The individuals in it are constantly changing in character. New animals are constantly added by birth and immigration and others are lost by death and emigration. Furthermore, as the central animal travels, his breeding population shifts also in geographic position, adding and subtracting animals from the population in so doing.

Since we have defined the breeding population as comprising those females with which John will mate (or would if he had time and opportunity) and the males which can mate with them, it follows that the breeding population is characterized by a genetical continuity and similarity, fluid and shifting, but unmistakable. Naturally, the elements of this population will not be genetically identical, even apart from sex differences. No natural population is. But the germ plasms of $John_n$ and $Jane_n$ and/or $Joan_n$ and/or $June_n$ are similar and compatible at least to the extent that they produce viable and fertile offspring, thus insuring the continuity of the population. Thus we have a moderately definable, natural, biological unit composed of animals which in nature will interbreed as the opportunity presents.

From John to Jane to breeding population we have a certain biological continuum, the individuals of the breeding population being connected, figuratively, by strands of germ plasm which represent this continuity. When we try to deal with larger aggregates of individuals, our categories become more and more abstract and empty of any real meaning. Our basic taxonomic unit is, of course, the subspecies. The best description available of a subspecies seems to be that it is a geographically (or ecologically) isolated subdivision of a species. This says little enough. From our point of view, a subspecies would be a geographically confined aggregate of breeding populations.

What, then, is a species? It would seem thus far to be the whole of any one series of breeding populations. This is certainly an innocuous-seeming definition, but is it? The definition as it stands unfortunately puts all living and fossil animals in one species, since there is a continuity of germ-plasm back from John to the original primordial cell, and from it forward to every living animal (not to mention plant). Thus, if we ignore time, we end up with only one species, which is all to the good insofar as it emphasizes the unity of life and the Brotherhood of Man, but is of little use to the practicing taxonomist.

Can we avoid the temporal difficulty? Let us redefine the species as the whole of any one series of breeding populations *as it exists at any one time*. This definition merely lands us in an exactly opposite difficulty, for we now have an infinity of species, time being infinitely divisible. Both these definitions of species at least have the advantage of being as objective as possible, but if we try to keep the definition of a species objective and still useful, we are forced to bring into the definition a discrete unit of time. As soon as we do this, we are, of course, being arbitrary, and perhaps not a little ridiculous. If we *should* define a species as the whole of any one series of breeding populations in existence over a period of 10,000 years, who is to say as to when the year zero is to be? Further, insofar as paleontology is concerned, no absolute time scale of usable "fineness" and precision is obtainable, and no cognizance is taken of differing evolutionary rates.

Thus, we come back to our original contention, that "species" have only a subjective existence. Our real biological unit is the breeding population, since it is through this ever-changing unit that the germ-plasm is passed. Taxonomy takes no notice of the breeding population, but any permanently useful taxonomic system must take account of its existence and its significance. Species and subspecies are the units with which the taxonomist deals, but they are merely convenient labels for arbitrary groupings and have only a minimum of biological meaning.

THE SPECIES CONCEPT: SEMANTICS VERSUS SEMANTICS

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The question whether or not species have objective reality is a perennial one. If a species were merely "a fiction, a mental construct without objective existence" one would expect under all circumstances the borderline between species to be exceedingly vague and subjective. However, if Dr. Burma should make an excursion into the neighborhood of his home town, he will find that every species of birds and mammals is sharply separated from every other one. This is not an exceptional situation; in fact it is the condition naturalists find in every part of the world. The primitive Papuan of the mountains of New Guinea recognizes as species exactly the same natural units that are called species by the museum ornithologist (Mayr, 1946). The arrangement of organic life into well-defined units is universal, and it is this striking discontinuity between local populations which impressed the naturalists Ray and Linnaeus and led to the development of the species concept. There can be no argument as to the objective reality of the gaps between local species in sexually reproducing organisms.

An excursion into the field of semantics appears helpful at this point. There are concepts that are absolute, like stone or fire, and others that are relative. If I meet an unknown man I do not know whether or not he is a brother. He is a brother only in relation to another person (a brother or sister of his). The word species likewise is such a relational term. It separates interbreeding populations from all others. In fact, the word species is most meaningful in connection with populations that are *not* conspecific, populations that are separated by a reproductive gap.

It has been pointed out (Burma, above) that it is virtually impossible to delimit a breeding population. Though many individuals are obviously members of a single effective, local breeding population, there are other individuals, more distant in space and time, which might possibly belong to different populations of the same species. It is not possible to undertake a clearcut delimitation of one breeding population of a species against others. This is no major tragedy at this point since we are not discussing the delimitation of breeding populations. What is important is the fact that there is *no* difficulty in delimiting a breeding population of one species against a sympatric-synchronous breeding population of other species. The gap between such species is well defined and has objective reality.

The presence or absence of a reproductive gap can be tested only where populations are in contact. The species thus has full objective reality only in a local fauna or flora. This *non-dimensional species* (Mayr, l.c.) is the standard of the species concept as originally conceived by Ray and Linnaeus. The objective reality of *this* species is beyond doubt.

To repeat once more, the essence of the species concept is the non-interbreeding of a population with other populations, a phenomenon which can be tested only where such populations are in contact. No matter how different certain individuals might be (polymorphs, larval stages, etc.), as soon as it is established that they are members of a single breeding population, they are considered conspecific.

The difficulties which Dr. Burma sees are not those of the original, non-dimensional species concept. Rather they are due to an expansion of this species concept in space and time. All species are subject to evolutionary change since, as Dobzhansky stated so truly, the species is merely a stage in an evolutionary process.

It is implicit in the theory of evolution that species should change in space and in time. There should be populations in an evolutionary series which are on the borderline between an ancestral and a daughter species. But even such a borderline population is as good a species in relation to others *with which it is in contact* as any normal species.

The difficulties to the practical application of the species concept caused by evolution are more apparent than real. There are gaps even in a multidimensional system. These gaps, as far as paleontologists are concerned, are caused by the extreme scantiness of the fossil record. The number of well described transformations of one species into another one is actually very small. Usually there is either a sequence of sharply discontinuous species as with the Eocene oysters of Texas (Stenzel, 1949) or else the sequence consists of slight subspecies, with even the extremes not yet having reached full species level. The fact that species are the product of evolution and continue to evolve seems only rarely to become a source of practical difficulties for paleontologists. In the majority of the cases the working paleontologist is dealing with a non-dimensional situation (as described above). In a single horizon at a single locality the species of the paleontologist are as well defined as are those of the local naturalist. Whenever a paleontologist runs into difficulties in such a non-dimensional system, it is not due to the weakness of the species concept but rather due to difficulties of taxonomic analysis (polymorphism, ecophenotypes, age variation, etc.).

The species concept has not only its greatest objective reality in a non-dimensional system, but also its greatest usefulness. In a sympatric-synchronous situation there is nothing intermediate between breeding populations and species. If a paleontologist studies a series of specimens from a given horizon, he knows that they are all either members of a single species or of different species. By definition there can be no intermediate stages in such a collection as, for example, subspecies. The species concept not only permits but actually demands an unequivocal decision. The species to be delimited in such cases by the practical taxonomist is by no means "a mental construct without objective existence," as claimed by Dr. Burma.

In all multidimensional situations an inference has to be made (Simpson, 1943) on the basis of the objective species of the non-dimensional system. The subjectivity of this expanded species concept by no means invalidates the species concept *per se*. The species of the local naturalist or of the paleontologist within a given horizon is clearly delimited against other species and can thus be considered as having objective reality.

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POSTSCRIPTUM

Benjamin H. Burma

At first glance it will seem that Dr. Mayr and I are indeed far apart in our conception of species. However, I believe that a close reading will show that our positions are actually not so very different after all. The neozoologist is usually impressed by the distinctness of the "species" he sees in the world today. On the other hand, the paleontologist is more likely to be impressed by the continuity of a given evolutionary line. Dr. Mayr's criticisms, I believe, do not actu-

ally attack the fundamental basis of my argument, the complete subjectivity of the concept of "species" when viewed in a four-dimensional space-time rather than in the unreal three-dimensional space of static time. They do focus attention on the practical utility of species as used by the neozoologist.

I cannot, however, agree that paleontologists are so uniformly impressed by the objective reality of species. It is true that in the past paleontologists seemed to have been little troubled by this. On the other hand, it is well to remember that many of the paleontologic species of fifty years ago are the genera and subgenera of today. The paleontologist of today finds it more and more difficult to recognize valid differences between the "species" of a given phyletic line as collecting and study become more thorough. It is this practical and growing difficulty which prompted my foregoing analysis of the species concept.

NOTES AND COMMENT

SUPPLEMENTARY NOTES ON *CREPIS* II. PHYLOGENY, DISTRIBUTION AND MATTHEW'S PRINCIPLE

ERNEST B. BABCOCK

In a recent number of this journal there appeared two stimulating discussions of evolution in *Crepis* * which were based on my monograph on this genus and which brought out several points of disagreement between my kindly critics and myself. Some of the points thus raised are of more general interest than the others and it is these that I propose to take up here. As for the other disagreements, I am willing to leave it for the careful reader of Part I of my monograph to decide for himself between the diverse opinions expressed in these two articles.

Phylogeny. As a basis for the present discussion, and to supply the lack of such a summary in the chapter on criteria in my monograph, the distinctions between primitive and advanced types in *Crepis* may be summarized as follows:

The *primitive* species are robust perennials with leafy stems, large simple or lyrate leaves, few large flower heads, unspecialized involucres with imbricate bracts which remain unthickened at maturity, and relatively large florets and achenes, the achenes all similar and beakless. The *most advanced* species are small delicate precocious annuals with nearly naked stems, small and often dissected leaves, numerous small flower heads with specialized involucres, the bracts being in two series, the outer series much reduced and the inner series thickened at maturity, relatively small florets and achenes, the achenes all similar or dimorphic, the inner ones at least being finely beaked.

Between these two extremes there exists an almost continuous series of forms representing various degrees of advancement. The 27 sections recognized by me are diagnosed by means of differentiating morphological characters. The phylogenetic relations between the sections, however, cannot be represented by a straight-line arrangement and hence the numerical order of the sections is necessarily somewhat arbitrary. Within each section the phylogenetic order of the species is determined primarily by the degree of reduction in the plant and its parts.

The difficult problem of determining the *most* primitive species was somewhat simplified by the discovery that the young seedlings of rhizomatous species develop a taproot, and that the rhizome develops secondarily from the caudex. This was reported in Appendix I (p. 160) of my monograph. Unfortunately this evidence that the taproot is more primitive than the rhizome was not obtained until after both Parts I and II of the monograph were partly in print. It was then too late to rearrange the order of the primitive sections. It was pointed out, however, that "although the most primitive species" (as determined from their morphology and their chromosomes, see p. 43) "have a rhizome, yet several taprooted species . . . are also very primitive." One of these taprooted species in particular, *C. pontana,* of Section VI, compares favorably with *C. sibirica,* the most primitive species morphologically of Section I, and both of these species have 5 pairs of chromosomes. However, most of the other rhizomatous species in Sections I–V have 6 pairs of chromosomes whereas the other three species of Section VI have 4 pairs. On the basis of chromosome numbers Sections I–V would remain the most primitive in the genus. But, as Stebbins points out, it may be assumed that the taprooted species with 6 pairs of chromosomes are all extinct. On this assumption, if morphology is to be used consistently as the primary criterion, then Section VI should become the first section, and this calls for a rearrangement of the primitive sections.

Crepis

Primitive Sections

Taprooted	Rhizomatous
1—VI (5, 4)	
	2—I (6, 5)
	3—II (6)
	4—III (6)
	5—IV (6, 5, 4)
6—VII (5)	
7—VIII (4)	
8—IX (5)	
	9—V (6)
10—X (5, 4)	

This suggested rearrangement of the primitive sections is shown in the accompanying table in which the section numbers as published in the monograph are set in Roman numerals and the proposed new numbers in Arabic numerals. The chromosome numbers (haploid or basic) for each section are shown in parentheses. In addition to the altered position of Section VI, Section V has been pushed onward to a posi-

* Clausen, J. Evolutionary patterns in the genus *Crepis.* Evolution **3** (2): 185–188. 1949.
Stebbins, G. L., Jr. Speciation, evolutionary trends, and distributional patterns in *Crepis.* op cit.: 188–193.

tion between IX and X because of the much greater reduction in size of the reproductive parts, especially the achenes, as compared with Sections I–IV. *Crepis* is believed to have been derived from *Dubyaea,* and *Dubyaea* contains both taprooted and rhizomatous species.

Distribution and Matthew's principle. Although the center of distribution for this genus is in the Mediterranean region and western Asia, as Clausen emphasized, nevertheless the evidence is overwhelming that the center of origin of the genus was to the north and east of the present center of distribution, as Stebbins admits. As soon as this is admitted one is practically driven to the selection of northern Central Asia as the center of origin for the reasons elaborately set forth in Chapters 5 and 6 of the monograph.

As for the question as to whether or not Matthew's principle can be said to apply to *Crepis,* it appears that one's opinion depends on the degree of rigidity with which the principle is formulated. It seems that too rigid a formulation can actually misrepresent Matthew's own concept of the *two* possible results which might follow from the operation of the general principle that the oldest (primitive) species of an evolutionary group will be pushed out into a peripheral region by the younger (advanced) species. For example, Stebbins asserts that "the application of Matthew's principle to *Crepis* as a whole would lead directly to the assumption that the genus *arose* (italics mine) in the eastern half of the Mediterranean region." This statement obviously is based on the facts that the present center of distribution for the genus is in this general region and that a certain amount of speciation has taken place there, together with the idea that, according to Matthew's principle, the most advanced species are *always found at the center of origin,* or center of dispersal in Matthew's terminology. Matthew, however, recognized that this is not necessarily the end result with respect to any particular group. This is clearly shown by the following quotation.*

"If the environmental conditions in the center of dispersal pass the point of maximum advantage for the race-type that is being developed and become unfavorable to its progress, we should find its highest types arranged in a circle around a central region, *which was the former point of dispersal* (italics mine), and the more primitive types arranged in concentric external circles. The central region will be unoccupied, or inhabited by specialized but not higher adaptations."

Now the Altai-Tien Shan region did become unfavorable to *Crepis* in late Pliocene and Pleistocene times. Only two primitive species are known to occur there now and they may have survived in favored niches. There are no advanced species—on the contrary these are confined for the most part to a narrow strip extending from southwest Arabia and Abyssinia northward across Africa and western Asia Minor and along the north shore of the Mediterranean Sea to western France. This strip, as seen on a north-polar projection of the earth (see p. 152 in monograph), roughly describes an arc of a circle with reference to the Altai-Tien Shan center.

Would Matthew have insisted that there be a *complete* circle of advanced species with reference to the primary center of dispersal before admitting that *Crepis* had conformed, at least in a general way, to his principle? I am inclined to think not. It seems more probable that, if he could have considered the long history of the genus and the many topographic features and climatic changes that limited its migration and determined its general trend of adaptation to drier conditions, he would not have hesitated to point to it as another illustration of the results of his basic principle, although with modifications from the simple ideal which are explainable in terms of changing environment.

Certainly it is the environment rather than the genetics of *Crepis* which has determined its present distribution pattern. If this be kept in mind, there should be no danger that anyone would be led to think that I had claimed to have confirmed Matthew's principle by means of evidence from modern genetics as Ownbey * seems to fear. Whether the apparent conformance with Matthew's principle in the present distribution of *Crepis* is merely coincidental, as Ownbey claims, or whether the basic *modus operandi* of that principle was actually operative, I am quite willing to leave for each interested student to decide for himself.

Just one more thought in this connection. No doubt Stebbins is justified in criticizing the impression given on pp. 141–143 of the monograph that 40 per cent (not nearly one-half as he states) of all the species in the genus migrated unchanged from Central Asia to their present locations to the west and south. Even though a thorough student like Hagen † reports the impression that in earlier geologic times an actual wave of desert plants flowed from Asia into the Sahara and took possession of it, the almost certain probability that evolution went on during the periods of migration should have

* Matthew, W. D. Climate and evolution. 1939. p. 32.

* Ownbey, M. The genus Crepis. Madrono 9: 165–168. 1948.

† Hagen, H. B. Geographische Studien über die floristischen Beziehungen des Mediterranean und Orientalischen Gebietes in Africa, Asien, und Amerika. Mitt. Geogr. Ges. in München 9: 111–222. 1914.

been emphasized by me. This idea *was* expressed more than once earlier in the monograph. For instance (p. 109): "Even the high montane *Crepis* species of southern Europe, *or their immediate ancestors,* are believed to have migrated from Central Asia."

This line of thought suggests the concept of a slowly expanding center of speciation for *Crepis* which migrated from northern Central Asia to the eastern Mediterranean region. Is it not possible that, in terms of this concept, the operation of Matthew's principle becomes even more evident?

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TOWARDS A MODERN SYNTHESIS

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It is a commonplace that the boundaries of the conventional biological disciplines are in the process of dissolution. One of the manifestations of this process has been the organization of the Society for the Study of Evolution, the aim of which is integration of the contributions to this study made by comparative anatomists, ecologists, geneticists, paleontologists, physiologists, systematists, and others. Such integration was notoriously missing in the past. In particular, the views of causation of evolution entertained by many paleontologists seemed flatly contradictory to, or at least difficult to reconcile with, those arrived at by geneticists. But as so often happened in the history of science, the contradiction arose not from incompatible findings but from incompatible languages used to describe these findings. It was a case of mutual unfamiliarity of paleontologists and geneticists with the attainments of the respective disciplines.

To G. G. Simpson belongs the leading role in the synthesis of the paleontological and genetic findings bearing on evolution. In his "Tempo and Mode in Evolution," published in 1944, he has convincingly demonstrated that paleontology has uncovered no facts contradictory to the known genetic principles. The theory of the mechanisms of evolution deduced from these principles is sufficient to account for the paleontological findings as well. In his book just published,[1] Simpson covers not only the ground dealt with in his earlier work, but in addition essays the formidable task of building a coherent philosophy of existence and ethics based on evolutionary doctrine. It is almost incredible that between the covers of this rather small book Simpson has not merely succeeded in summarizing all the important attainments of modern evolutionary thought, but has made it without resort to the technical and cumbersome language which makes most scientific books accessible only to the initiated. This book can be called "popular" in the best sense of the word. It is not "popular" because it "talks down" to the reader, or because it tries to create a so-called "human interest story." It does nothing of the kind. Despite many flashes of genuine wit and humor, the book requires concentration of attention and sincere intellectual effort on the part of the reader. But granted these things, the book can be read and understood in its entirety by those not previously familiar with either paleontology or genetics, in other words, by intelligent laymen. At the same time, paleontologists and geneticists will not be able to skip many pages as being too familiar or too trite.

It would be futile to attempt to summarize a book so rich in content even in a long review. The following quotations are intended only to convey an idea of the extraordinary breadth of its scope. The keynote is sounded in the following sentence: "For the reader who may have browsed widely in the literature of evolution and who may have become bewildered by continuing divergencies of opinion, here is a touchstone: I think it fair to say that no discussion of evolutionary theory need now be taken seriously if it does not reflect knowledge of these studies [of population genetics] and does not take them strongly into account." Simpson's views of the bearing of evolution on philosophy and ethics are epitomized in the following paragraph which has the ring of a peroration: "Man has risen, not fallen. He can choose to develop his capacities as the highest animal and to try to rise still further, or he can choose otherwise. The choice is his responsibility, and his alone. There is no automatism that will carry him upward without choice or effort and there is no trend solely in the right direction. Evolution has no purpose; man must supply this for himself. The means of gaining right ends involve both organic evolution and human evolution, but human choice as to what *are* the right ends must be based on human evolution. It is futile to search for an absolute ethical criterion retroactively in what occurred before ethics themselves evolved. The best human ethical standard must be relative and particular to man and is to be sought

[1] SIMPSON, G. G. 1949. The meaning of evolution. Yale University Press. xv + 364 pp.

rather in the new evolution, peculiar to man, than in the old, universal to all organisms. The old evolution was and is essentially amoral. The new evolution involves knowledge, including the knowledge of good and evil."

The appearance of Simpson's book is now particularly timely, because of the recent upswing of vitalistic or finalistic speculation about evolution. Lecomte du Noüy's "Human Destiny" has achieved a best seller success despite its being one of the crudest examples of this scientifically retrograde current. The recent work of Vandel [2] is a far more subtle and refined specimen of the same genre. Now, the stock argument of the finalists has been that the course of evolution disclosed by paleontological findings indicates orthogenetic striving to reach foreordained goals, which is inexplicable by mutation, recombination, and natural selection based, allegedly, on "blind" chance. Simpson accomplishes more than exposing the fatuity of finalism. His book shows that we are approaching a real synthesis of the evolutionary thought which may serve as a scientific basis of ontology and of ethics. This is perhaps the most daring vision which ever challenged the creative imagination of a biologist.

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[2] VANDEL, ALBERT. 1949. Invention et Finalité en Biologie. Gallimard, Paris. 201 pp.

A SYNOPSIS OF CONTEMPORARY EVOLUTIONARY THINKING [1]

ERNST CASPARI

The present volume comprises a series of lectures given at the Bicentennial of Princeton University. All of them are concerned with the topic of evolution in one of its different aspects, the authors being specialists in genetics, taxonomy and paleontology. The volume deals with exactly the same problem to which the present journal is devoted, the synthesis of the facts of genetics, taxonomy and paleontology into one unified picture of evolution.

The book consists of 23 independent articles, different both in content and in manner of presentation. Besides being concerned with different aspects of the problem, their character ranges from general discussions to concrete specialized presentations such as *Spencer's* paper on the homology of genes in two species of Drosophila, and *Westoll's* discussion of the evolution of Dipnoi. The reader will find this change in general character of the papers interesting and stimulating. The same may be said concerning the fact that the papers are collected from three different fields of biology. The reviewer, being a geneticist himself, was particularly interested in the paleontological papers with whose material he was least acquainted, and he suspects that many readers will react in a similar manner.

The renewed interest in evolution which characterizes the last decade is due to the elaboration of the Neo-Darwinian theory by taxonomists and geneticists independently and to its wide acceptance by biologists, thanks to the widely read books by *Dobzhansky* and by *Mayr*. This ended a stalemate in evolutionary thinking which, according to *Mayr's* contribution in the present volume, was due in part to the anti-evolutionary attitude of early geneticists. It seems to the reviewer that the arguments of some of the older Darwinists trying to explain the adaptive value of particular traits in particular organisms was a contributing factor in discrediting evolutionary speculations since some of these arguments appeared farfetched to the unbiased reader. Both of these attitudes were based on the same fundamental mistake: that traits were judged according to their adaptive value for the individual organisms, instead of considering their influence on the structure of populations.

Neo-Darwinian thinking started out with the consideration that evolution deals with statistical changes in populations. *Wright* has considered changes in gene frequencies in populations as the fundamental evolutionary phenomenon, and has developed a complete statistical theory which accounts for a large number of known facts, and predicted the presence of others which have since been established. In his contribution to the present volume he reviews his own work, and gives a consistent picture of the processes of evolution and of adaptation in statistical terms. This lecture may be taken as the central chapter of the book, since the other genetic and taxonomic papers are elaborations of certain aspects of the theory, or interpretations of actual cases in the light of the theory. *Moore's* remark that "evolutionary theory contributes more to the understanding of the data than the data contribute to an unstanding of evolution" is typical for this feeling about the central importance of the Neo-Darwinian theory.

While the facts known to geneticists, and the distribution of organisms in space and their

[1] Genetics, paleontology and evolution. Edited by Glenn L. Jepsen, George Gaylord Simpson and Ernst Mayr. xiv + 474 pp. Princeton University Press, 1949.

adaptation to their environment are generally considered to be in good agreement with the Neo-Darwinian theory, paleontological findings have for a long time been interpreted under a Lamarckian theory. *G. G. Simpson* was the first paleontologist to apply Neo-Darwinian theory consistently to paleontological facts, and his paper and the paper by *Romer* in the present volume demonstrate clearly that no reason exists not to apply this theory to paleontological data. Six of the lectures deal with specialized paleontological topics, most of them with vertebrates, and it is in these that some of the reasons for the difficulties can be found. Hardly any mention is made of invertebrate paleontological material.

The paleontologist observes structural changes only. Furthermore, in many cases, e.g. in the Taeniodonts discussed by *Patterson,* he works with numerically restricted and incomplete material. Therefore, statistical treatment of paleontological material appears to have been attempted only recently. *Romer,* in describing the evolution of the teeth of horses, and *Westoll,* in discussing the skulls in a large population of Dipterus, mention a conspicuously high variability in times of fast evolutionary change. This phenomenon could be understood either as a consequence of a variable genetic background (*Simpson*) or by incomplete "buffering" of cell-physiological and developmental reactions (*Stern*), two interpretations which do not exclude each other. It may be possible that changes in variance of populations in time might give some evidence concerning "genetic rates" of evolution which must be supposed to lie at the basis of the observed morphological and taxonomic changes.

The classical paleontological procedure consists in describing structures in terms of comparative morphology. Evolution is consequently described as changes in morphological structures in time as compared either with the oldest member of the series or with deduced "primitive" conditions. It is usual, even when a large number of specimens exists, to treat one of them as the type, and the others as variants of the type. Evolution is therefore frequently described as gradual changes in type. It is found, in this way, that usually a number of characters vary concomitantly which gives the impression of orthogenetic or directed evolution. This has given rise to the acceptance of Lamarckian ideas by many paleontologists. The actual case histories described in the volume, such as the Labyrinthodontian skull (*Watson*), the Dipnoi (*Westoll*), Taeniodonts (*Patterson*) and numerous others, are all described in terms of directed evolution, more precisely in terms of directed changes of types in time. This does not mean, however, that the authors of these articles subscribe to Lamarckian concepts. On the contrary, all of them seem to be convinced that orthogenetic evolution is caused by "orthoselection," i.e., by increasingly perfect adaptation to a particular ecologic situation. It is usually possible to describe a large number of directed structural changes as direct consequences of a primary trend of selection, e.g., the changes in the structure of the legs and teeth of the horses are considered to be consequences of the gradual increase in size (*Watson*). But this, in some cases, leaves open the question of the origin of the primary adaptive feature, e.g., the flattening of the skull in Labyrinthodontia and the acquisition of digging claws in the Stylinodontinae (*Patterson*). The former is ascribed to "internal conditions," the latter to a single orthodox mutation which preadapted the animal to a different ecological niche. It is just in this type of question that the greatest amount of difference of opinion is found. *Davis,* e.g., denies the occurrence of preadaptation, and *Muller* prefers to believe that quantum evolution does not actually occur. It appears possible that many of these cases may be resolved more easily if it is considered that selection does not act on isolated structures, or animals carrying structures, but that it acts on populations selecting not for individual genes but for gene combinations. A possible interpretation of quantum evolution in terms of populations is suggested by *Romer.*

Romer attacks one of the most widespread remnants of Lamarckist thinking in evolution, the moralistic connotations of such terms as racial sterility, degeneracy and racial old age. It might be mentioned in passing that a similar moralistic tendency seems to appear in Neo-Darwinian thinking, particularly in discussions of aberrant types of reproduction such as hermaphroditism, asexual reproduction and obligatory autogamy.

The wealth of interesting and stimulating material contained in the volume is very large, and the reviewer regrets that he does not have the opportunity even to mention some of the chapters which he enjoyed most. Since, however, the volume represents in monumental fashion a survey of contemporary evolutionary thinking, it seemed preferable to call attention to the main points in which agreement and in which disagreement prevails between the main biological disciplines.

The book closes with a summation by *H. J. Muller* in which the main points brought out in the previous discussions are synthesized into a comprehensive and convincing picture of evolution. Added are an index and an extensive glossary which is very useful since most readers will not be equally conversant with the terminologies of the different disciplines represented in the book.

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CHROMOSOMES OF THE VERTEBRATES[1]

M. J. D. WHITE

In view of the wide dispersal of the literature on animals cytology, it is regrettable that so few monographs on the cytology of particular groups have been written. Thus the taxonomist who wishes to ascertain the extent of cytological knowledge concerning the particular group he is interested in is almost always at a loss to know where to look. A perusal of the few lists of chromosome numbers that have been published is uninspiring, since these catalogs are all out-of-date, seriously incomplete, in some cases full of inaccuracies and do not distinguish between reliable modern work and the completely valueless determinations of some of the earlier workers.

For these reasons, Prof. Matthey has rendered a real service to mammalogy, ornithology, herpetology and ichthyology, as well as to cytology, by surveying the literature on vertebrate chromosomes in a comprehensive and critical manner. Having contributed over thirty-five articles to that literature in the past twenty years, Matthey has a record of achievement in the field which entitles him to speak with authority. It is greatly to be hoped that the publication of his book will inspire others to attempt similar monographs on the comparative cytology of the Diptera, Orthoptera, Graminaceae and other groups on which a large amount of cytological work has been carried out. Such monographs would be of inestimable value to all serious students of evolution.

It is now absolutely clear that the vertebrates (with the exception of a few groups such as the Urodeles) are extremely unfavorable material for detailed cytological work. The difficulties arise partly from the fact that the chromosome numbers are usually high and the individual chromosomes extremely small; an even greater source of error and confusion, however, is the tendency of the chromosomes to clump together in aggregates if the fixation has not been quite perfect. For this reason the chromosome counts of the earlier workers were in most cases far too low and their accounts are now known to be quite valueless since they had no objective criteria to distinguish good from bad fixation. Matthey's greatest contribution to vertebrate cytology is probably his insistence on impeccable fixation, the technical methods employed for dehydrating, embedding and staining the material being of secondary importance.

To a considerable extent the technical obstacles to reliable work in the field of vertebrate cytology still persist today, although the work of Matthey and of the Japanese school (Oguma, Makino, Minouchi, Yamashina and others) has led to a considerable improvement in the situation. In the birds, however, these obstacles are still very serious. Thus the student of avian speciation must, for the present, resign himself to the fact that he cannot use the method of comparative cytology, which has proved so valuable in other groups, simply because the technical obstacles do not permit us to arrive at an absolutely accurate morphological description of the chromosome set of any species of bird (the position as regards the mammals and reptiles is substantially better, but not entirely satisfactory even yet).

One fact which emerges very clearly from Prof. Matthey's book (and which would be equally evident in any similar survey of the cytology of molluscs, insects or any other group of animals) is that variation in chromosome number is by no means at random. Thus particular groups (families, orders or classes) tend to have particular "type numbers" or "modal numbers" around which variation occurs only to a limited extent. As an example we may cite the Urodeles, where the families Hynobiidae and Cryptobranchidae have high numbers (20–32 chromosome pairs), while the Salamandridae, Plethodontidae, Amblystomidae and Proteidae have much lower numbers (12–14 pairs). In the mammalia the Eutheria show, in general, much higher numbers than the marsupials. It has frequently been suggested in the past that groups with high chromosome numbers have arisen from ones with low numbers by polyploidy and one recent author has even based his views on human genetics on the assumption that man is a tetraploid organism. No critical evidence has ever been presented in support of these hypotheses and Prof. Matthey obviously does not attach any importance to them, considering that, in general, the more primitive groups have higher chromosome numbers (although admitting that no general rule exists on this point).

Although the vertebrates exhibit rather considerable variation in chromosome morphology from group to group, their cytology is otherwise rather uniform. A sufficient number of studies have been carried out on the meiosis of all the main classes to make it clear that the meiotic mechanism is invariably orthodox, there being nothing comparable to the bizarre genetic systems of the scale insects, gall-midges or hymenoptera. We may safely predict, on the basis of the cytological evidence, that all spe-

[1] Les Chromosomes des Vertébrés: by Robert Matthey. 356 pp., 48 text figures and 35 plates (442 figures). Lausanne, F. Rouge, Librairie de l'Université. 1949. 48 Swiss francs.

cies of vertebrates show crossing-over in both sexes.

Apart from the study of the genetic systems of organisms by cytological means there are three main ways in which comparative cytology can contribute to a better understanding of the factors of evolution. One is by a straightforward morphological comparison between the chromosome sets of related species, a second is through cytological analysis of hybrids, the third is through the study of intraspecific chromosomal polymorphism (where present). The first type of study has led Matthey to attach much importance to transpositions of whole chromosome arms in evolution, i.e. structural changes whereby two rod-shaped chromosomes are replaced by one V or vice-versa. He calls such evolutionary changes "Robertsonian" after the American cytologist, W. R. B. Robertson, a student of C. E. McClung, who emphasized their importance in the Orthoptera. As a logical consequence of this attitude he considers the number of major chromosome arms in a species (excluding the minute "second arms" of acrocentric (rod-shaped) chromosomes) as a more important constant that the actual chromosome number. The difficulty here is to decide what chromosome arms are sufficiently minute to be legitimately excluded from the *"nombre fondamental"* or number of major chromosome arms. In certain species the distinction between metacentric and acrocentric elements in the chromosome complex is absolutely clear-cut, but in others intermediate types of chromosomes occur (i.e. J-shaped elements in which the shorter limb may be one-tenth or less of the length of the longer arm). Such cases make the concept of a "nombre fondamental" of doubtful validity. Even in the Diptera and the Orthoptera where the material is infinitely more favorable for a cytological analysis than in any vertebrate, we are still a long way from understanding just how the visible differences between the chromosome sets of related species have arisen, by structural rearrangements, in the course of evolution. It is, however, clear that the "Robertsonian" evolutionary transformations are only one type of structural change that has occurred, the easiest to detect, perhaps, but not necessarily the most frequent. The conclusion to which the reader is inevitably forced after perusal of Prof. Matthey's book is that the processes of chromosomal evolution are so complex that we can only hope to understand them by making the fullest use of the most favorable material. Strategic considerations should cause serious investigators to avoid vertebrate material for chromosome work in the future, except in special cases.

A considerable number of artificially-produced interspecific hybrids are now known in the vertebrates, having been obtained in zoos, aviaries, aquaria, and in the course of agricultural breeding work. There are also a few instances in which undoubtedly distinct species of vertebrates are known to hybridize in nature. It is to be regretted that so few of these cases have been investigated cytologically. Even the mule, the best-known of all hybrids, has not been studied cytologically since the very early days of vertebrate cytology when only the most primitive technical methods were employed.

In many groups of the invertebrata various types of chromosomal polymorphism exist in natural populations of the same species and are open to cytological analysis. Thus in *Drosophila* spp. inversions are frequent, while in grasshoppers supernumerary chromosomes, centric fusions, centromere shifts and translocations may all exist in a state of flux in the wild populations, either singly or in various combinations. Studies on these types of natural polymorphism have thrown much light on general biological problems such as the nature of species, the mechanisms of adaptation to the environment and the dynamics of natural selection. It is therefore regrettable that, with very few exceptions, no situations of this kind appear to have been recorded in the vertebrates. One interesting one, however, seems to exist in a lizard, *Gerrhonotus kingi*, where Matthey has shown that two rod-shaped chromosomes are sometimes, but not always, fused to form a V. Thus some individuals possess a pair of V's at meiosis, while others have a V and two rods (theoretically, individuals with four rods should exist as well, but have not yet been found). No doubt other types of chromosomal polymorphism exist in many species of vertebrates, but the unfavorable nature of the material makes their detection very difficult.

Most of the workers in the field of vertebrate cytology have been particularly interested in sex chromosomes. In spite of some earlier accounts which must now be disregarded, it is now clear that none of the fishes or amphibia possess morphologically differentiated sex chromosomes, i.e., their X and Y chromosomes are cytologically indistinguishable and cytological studies cannot be used to determine which sex is heterogametic (there is now genetic and experimental evidence proving that some fishes and amphibia have male heterogamety, while in other species the female is the heterogametic sex). One of the outstanding facts about the comparative cytology and genetics of the vertebrates is that the mammals invariably show male heterogamety (having strongly differentiated X and Y chromosomes which can easily be distinguished cytologically), while in the birds female heterogamety is probably universal (Prof. Matthey is skeptical as to the validity of the cytological evidence on this point,

but the genetical evidence is clear in several species). One would very much like to know the position in the various orders of Reptiles, particularly in view of the fact that the Turtles are suspected, on morphological grounds, of being somewhat closer to the mammalian stock than the other reptiles. Unfortunately, the cytological evidence on this point is conflicting. The Japanese school of cytologists claim to have established the existence of female heterogamety in three species of lizards and a species of tortoise, one small chromosome in the female set being unpaired. Prof. Matthey casts grave doubt on the validity of these observations (which, if taken at their face value, would indicate an XX (♂) : XO (♀) mechanism), his own observations on a number of species of Reptiles suggesting that the chromosome sets of the males and females are morphologically identical, so that the X and Y, whichever sex they are present in, are presumably of the same size and shape. Genetical evidence on this point is, of course, also lacking, the Reptiles being singularly ill-adapted for breeding work.

In view of their isolated systematic position, one would also very much like to know where the Monotremes stand in regard to heterogamety. It was with a view to settling this question that the present reviewer made some sections of an *Echidna* testis some years ago. The results were disappointing, since no meiotic divisions were encountered. A few spermatogonial mitoses did, however, show that the chromosome number was extremely high, many of the chromosomes being very minute. The general picture was thus similar to that seen in the birds and reptiles rather than that found in the mammals. In particular, there was not the slightest resemblance to the marsupials, which have relatively low chromosome numbers. More recently Prof. Matthey seems to have had a very similar experience with some material of *Ornithorhynchus*. In neither case were sex chromosomes identified, but in view of the poor fixation of the material, this was inevitable. The problem of the heterogamety of the Monotremes is thus still unsolved.

The Mammals are thus the only class of vertebrates in which the sex chromosomes can definitely be identified with complete certainty. In the vast majority of the species so far studied the males are XY, the females XX, but it is possible that in a few species the Y chromosome has been lost from the male sex, which has an odd diploid number. The cover of Prof. Matthey's book carries a figure of the giant sex-chromosome pair of the mouse *Microtus agrestis*, discovered by the author after the book was in press. Although it is still not quite certain whether some mammals have become XO in the males, it is undeniable that at least two species (*Sorex araneus* and *Macropus ualabatus*) have acquired multiple sex-chromosome mechanisms ($X_1X_2Y : X_1X_1X_2X_2$ or $XY_1Y_2 : XX$) as a result of translocations between sex chromosomes and autosomes (although the precise mode of origin of these mechanisms cannot be stated definitely).

In a review of this kind it is not possible to do justice to the many excellent features of "Les Chromosomes des Vertébrés" but a brief mention should be made of the interesting discussion on the cytological evidence concerning the relationships of the various groups of lizards. A noteworthy addition to the book is the atlas of 442 figures of metaphase plates. Non-cytologists will, however, be somewhat at a loss to determine which figures represent the diploid sets and which represent meiotic metaphases and will find no guidance in the legends.

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COMMENTS ON EVOLUTIONARY LITERATURE

Ernst Mayr

Many readers of Evolution have requested that a section with reviews and abstracts of the current evolutionary literature be made a regular feature of the journal. This has been impossible so far, for practical reasons, but in the present issue a few papers shall be discussed that have lately reached the Editor's desk. If it is considered useful, this section will be continued in future issues.

Species in paleontology.[1]—In the nineties of the last century every ornithologist would have agreed that species are something purely subjective. There were all kinds of species, such that were strikingly different and such that were only slightly distinct. There were some that divided into a few slight subspecies while most were monotypic. New populations were found daily which differed slightly from the type of the most similar species, and so they were described as new species. Ornithological taxonomy, as dominated by the typological species concept, was confused, if not chaotic. The species was merely "a fiction, a mental construct without objective existence," as Dr.

[1] J. Hough. 1949. The subspecies of *Haplophoneus:* a statistical study. J. Paleont., **23**: 536–555.

Burma would put it. Then came the introduction of the biological species concept leading to the widespread recognition of polytypic species. Rensch has described dramatically how this revolutionary change of the species concept reestablished order from chaos and led to the well-defined "objective" species recognized by the taxonomist of recent birds. Nineteen intergrading or very similar species of Palearctic nuthatches were found to belong to four well-defined species, eight South American species of sparrows to the single polytypic species *Zonotrichia capensis*.

Large areas of paleontology are in the condition in which ornithology was in the 1890's. However, analysis has now reached the point where synthesis can be attempted. Seven species of saber-toothed cats of the genus *Haplophoneus* are shown by J. Hough (extending a previous study of Simpson) to belong to a single species with two subspecies. Two additional insufficiently known "species" represent apparently a third subspecies. A close scrutiny of recently published papers on foraminifera and other fossil invertebrates convinces me that they also are still in the condition in which the species of birds were in the 1890's.

Vigorous efforts are now being made by younger paleontologists throughout the world to separate the wheat from the chaff, to apply consistently trinomials to populations that do not deserve species rank, and to replace the typological species concept by a biological one. It can be predicted that this development will lead to a lessening, if not elimination, of the differences that now exist between the species of the paleontologist and that of the neontologist.

Again homology.[2]—The author points out—as have several others recently—that the term homology can neither be discarded nor be defined identically in all cases where it is employed. The roots of the homology concept of Owen (and of such later authors as Naef and Kälin) in the typological philosophy of Plato are emphasized (following Lubosch, 1931).

Paleontology from Cuvier to the present.[3]—The Swiss paleontologist E. Kuhn presents a well-informed survey of the present concepts of paleontology. His views appear to be, on the whole, similar to those of Simpson and Rensch.

Evolutionary contributions of paleontology.[4]—The veteran paleontologist Stromer presents here what he considers as indisputable results of paleontological research. He organizes his material in the form of twenty-four theses which are discussed and backed by an abundant documentation. This latter feature of Stromer's contribution is perhaps the most valuable to many students because it supplies a subject-indexed catalog to the widely scattered paleontological literature on such questions as gigantism, reversal of evolutionary trends, rates of evolutionary change, former climates, eruptive evolution, relation between plant and animal evolution, polysomerism and anisomerism, trend toward greater mobility, specialization, evolutionary progress, and many others. He states that he preceded Williston in the establishment of the rule, now often referred to as Williston's Rule.

Speciation in a specialized niche.[5]—In all classes and phyla of animals it may happen that a species finds an aberrant but otherwise particularly suitable niche and that this species becomes the ancestor of a prosperous new category. Among the protozoans the peritrichan ciliates have found the surface of other larger animals a very favorable habitat. A single investigator found no less than 129 species (62 of which were new!) attached to the outside of about 110 species of larger fresh-water animals. Many species of *Peritricha* seem to be species specific; in fact the occurrence of two sibling species of turbellarians in England was recently discovered owing to differences in their peritrichan fauna. Not being as devoid of external characters as are most parasites, peritricha may be particularly favorable material for a study of the evolution of host-commensal relationships.

Speciation in oceanic beetles.[6]—The three main islands of the Tristan da Cunha group in the South Atlantic (Tristan d. C., Inaccessible, Nightingale) are an evolutionary microcosmos, like the Galapagos or Hawaiian Islands, only to a much lesser degree. In a report on the beetles of this group, three subjects are discussed in particular: winglessness, speciation, and faunal origin.

Only two of the twenty endemic species have normally developed wings. Wing reduction is due to elimination of winged types by being blown away, coupled with normal mutation pressure.

Nine species were introduced by man and have a wide distribution. Twenty species are endemic, belonging to nine genera. There has been pro-

[2] H. Szarski. 1949. The concept of homology in the light of the comparative anatomy of vertebrates. Quart. Rev. Biology, **24**: 124–131.

[3] E. Kuhn. 1948. Der Artbegriff in der Paläontologie. Eclogae geol. Helv., **41**: 389–421.

[4] E. Stromer. 1944. Gesicherte Ergebnisse der Paläozoologie. Abh. Bayer. Akad. Wiss.—Math. Naturw. Abt., N. F. Heft 54, 114 pp.

[5] N. Nenninger. 1948. Die Peritrichen der Umgebung von Erlangen mit besonderer Berücksichtigung ihrer Wirtsspezifität. Zool. Jahrb. (Syst.), **77**: 169–266, 4 plates.

[6] P. Brinck. 1948. Coleoptera of Tristan da Cunha. Results Norv. Sci. Exped. Tristan da Cunha 1937–1938. No. 17, 122 pp.

nounced speciation in the genus *Tristanodes*. The geographical nature of this speciation is brought out in the following tabulation.

Tristanodes

Species Group + Species	Tristan	Inaccessible	Nightingale
integer group			
integer		+	
sivertseni			+
attai group			
attai	+		
medius		+	
minor			+
craterophilus group			
craterophilus	+		
echinatus		+	
insolidus			+
reppetonis group			
scirpophilus	+		
reppetonis		+	
conicus		+	

Except in the *reppetonis* group all are strict geographical representatives. Tristan apparently has lost some endemic species owing to habitat destruction by man.

Speciation in Turkish fishes.—The continuing drying out of lakes that had originated in the moister phases of the post-Pleistocene is apparently a worldwide phenomenon. Hubbs and his students have shown how the resulting isolation of populations in relic lakes and springs has stimulated speciation in Western North American fishes. Kosswig and his students have shown in a series of papers that similar conditions prevail in Asia Minor. Aksiray[7] discusses the geographical variation of the ten species of cyprinodonts known from Anatolia. *Aphanius chantrei* has eleven subspecies in southern Anatolia. Various populations of *Anatolichthys transgredius* which occur in various springs on the shores of a single lake differ significantly in scalation and proportions. It is implied that these differences are very recent.

Speciation in salamanders.[8]—This work of 150 pages with many figures and two colored plates is the most thorough analysis ever made of the geographical variation of a single species of salamander. What were currently considered four or five species are shown by R. Stebbins to be merely highly divergent races of a single polytypic species with seven subspecies. These range from British Columbia in the north to southern California. In California there are two series of races, separated by the unsuitable San Joaquin Valley. One series follows the coastal ranges down to San Diego Co., the inland chain follows the Sierra Nevada southward. The ring of races is closed south of the San Joaquin Valley in the mountains of southern California. But here a uniformly reddish brown subspecies (derived from the coast range chain) and a subspecies that is contrastingly spotted orange and black co-exist side by side without evidence for intergradation. Evidently here is another case of "circular overlap." Intergradation is complete north of the San Joaquin Valley.

There are extensive areas of intergradation between nearly all of the subspecies; in fact in some cases the range of the "pure" subspecies appears smaller than the zone of intergradation. The areas of intergradation coincide with regions of low relief and appear zones of reduced gene flow. However, the author doubts that they are zones of secondary intergradation. His arguments on this point are not completely convincing. There have been periods in the recent past that were considerably more arid than the present. Why should not some of the ranges be broken at that time that are even now rather tenuous? Stabilized hybrid populations are by no means necessarily more variable than ordinary subspecies.

Stebbins devotes a good deal of attention to the question whether or not the morphological characters of the various races are of selective significance. This he believes to be able to show for the amount of melanin and of lipophores and guanophores. There are clinal changes in these characters correlated with gradients relating to humidity and light. As far as the reduction of melanin from a high in the coolest and most humid region toward the hotter and more arid regions is concerned, the author indicates that it cannot all be explained on the basis of cryptic coloration on various soil types. At least as important is the fact that infra-red absorption by melanin is of selective advantage in cool regions, but is selected against in hot regions. Additional factors, such as thyroid activity, may contribute to the difficulty of analysis.

These are merely a few highlights of a thorough and thoughtful study.

Man as a biological phenomenon.[9]—The Swiss zoologist Portmann has for years concentrated on an aspect of embryology that is usually much neglected, namely the development of the late embryo and newborn vertebrate. These studies

[7] F. Aksiray. 1948. Rev. Fac. Sci. Univ. Instanbul, Ser. B. T., **13**: 97–138, 280–310.

[8] R. C. Stebbins. 1949. Speciation in salamanders of the plethodontid genus *Ensatina*. Univ. Calif. Publ. Zool., **48**: 377–526, p. 11–16, 16 text figs.

[9] A. Portmann. 1944. Biologische Fragmente zu einer Lehre vom Menschen. Benno Schwabe and Co., Basel, 141 pp.

are important for the evolutionist because they are comparative studies, bringing out the differences between various kinds of reptiles, birds, and mammals and their adaptive significance. Portmann, in the present account, emphasizes the very specialized position of man. The human baby is much more helpless than the newborn of an arboreal anthropoid, but has a much less developed habit of clinging to the mother. The anthropoids in their actions and the development of their nervous system at birth are much closer to the groups with precocious young, like the ungulates, whales, and seals, than to the groups with helpless, blind young, like rodents, insectivores, and most terrestrial carnivores. Nevertheless the human baby has secondarily become nearly as helpless as a young kitten, this in spite of its much greater weight than that of the newborn anthropoid. This great body weight is correlated with a heavy brain at birth while the post-natal growth of the brain (3.6–3.9 ×) is hardly greater than in the anthropoids (3.0–3.6). Portmann discusses these facts and many others without focussing very clearly on their adaptive and evolutionary meaning.

Allometric physiology.—Huxley, Rensch, Newell, and others have shown that body proportions during the life cycle of the individual as well as in evolutionary series usually show an allometric relationship to body size. It has been suggested by Rensch that—as far as evolutionary sequences are concerned—much of allometric growth of specific organs is related to their function. Adolph [10] extends this thought to a direct measurement of physiological processes in relation to body size. He shows that if the rate of water intake, basal oxygen consumption, urea clearance, or any of thirty other other physiological factors is compared with body size, it obeys the good, old $X = aY^b$ formula. Among mammals, when the log of the physiological factors of various species was plotted against the log of body weight, the respective points were rather neatly arranged along a straight line. The emphasis of Adolph's study is on the closeness of this correlation. Interesting as this is, the evolutionist is, as Rensch points out, almost more interested in the cases where an organ (or physiological process) can escape the straight jacket of size allometry. Evolutionary advances are presumably always connected with such changes in the factors *a* and *b*.

Measuring differences between samples.[11]—Students of natural populations are always searching for new statistical methods to express the differences between natural populations or between samples from such populations. The statistical method of the experimenter is to calculate the probability that two or more samples were drawn from the same population. It seems slightly absurd to apply this method to samples of natural populations that are known to be distinct. A number of suggestions for more direct methods have been made. In the present paper the author demonstrates step by step the calculations of Hotelling's method of multivariate analysis. Even more general than this method is the one by Mahalanobis which was discussed by Fisher some years ago (1938, Ann Eugenics, vol. 8, pp. 376–386).

Sorting out populations.[12]—Every student of populations encounters sooner or later a strongly bimodal curve and realizes that he is actually dealing with a mixed sample of two populations. Up to now there was no simple method available to find the statistics (particularly mean and standard deviation) of the involved populations. Harding describes how this can be done with the help of a special "probability graph paper" which is commercially available. The method is, incidentally, also suitable for a quick graphical determination of standard deviations as well as for a rough test for the normality of the distribution of small samples. However, the method is most useful when large samples are available.

Mass collections in orchids.[13]—The Hebridean populations of four species of *Orchis* were analyzed. There is much interfertility and the occurrence of natural hybrids, even though two of the species are polyploids. Two of the species are fairly uniform throughout the area, a third breaks up into a number of local races and subspecies. Individual variability is not clearly correlated with frequency of occurrence in various parts of the range.

Selection and mimetic polymorphism.[14]—Next to *Papilio dardanus* the most remarkable mimetic butterfly is the African nymphalid *Pseudacraea eurytus*. The degree of its polymorphism is indicated by the fact that Carpenter recognizes and describes no less than thirty-three separate

[10] E. F. Adolph. 1949. Quantitative relations in the physiological constitutions of mammals. Science, **109**: 579–585.

[11] B. H. Burma, 1949. Studies in quantitative paleontology. II. Multivariate analysis—a new analytical tool for paleontology and geology. J. Paleont., **23**: 95–103.

[12] J. P. Harding. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Marine Biol. Assoc., **28**: 141–153.

[13] J. H. Harrison. 1948. Field studies in *Orchis* L. I. The structure of Dactylorchid populations on certain islands in the Inner and Outer Hebrides. Trans. Proc. Bot. Soc. Edinburgh, **35**: 26–66.

[14] G. D. H. Carpenter. 1949. *Pseudacraea eurytus* (L.): A study of a polymorphic mimic in various degrees of speciation. Trans. R. Ent. Soc. London, **100**: 71–133, 8 plates.

color forms in this species. Many of these are confined to rather small portions of the range, but up to twelve or more may occur in a single locality. Each type of *eurytus* mimics some species of the acraeid genus *Bematistes*. Male and female *Pseudacraea* are usually quite different and both are mimics. Seven handsome, colored tables show the range of variability. Normally the mimics are much in the minority, as compared with the model. However, *Bematistes* are rare on some islands in Lake Victoria and there is less opportunity for selection to operate. Interestingly enough there are on these islands many intermediates between the mimicking forms. Their frequency is almost exactly inverse to the relative frequency of *Pseudacraea*. On the mainland mimics are 18 per cent and specimens which depart from strict likeness to the models 4 per cent. On the three islands on which models are rarest the figures are: 62.3 per cent *Pseudacraea* of which 34.9 per cent are poor mimics, 68.5 per cent and 53.7 per cent, and 73.4 per cent and 56.2 per cent. The rapid rise in the number of intermediates as soon as selection relaxes is interesting in view of Goldschmidt's hypothesis of the origin of mimetic polymorphism. In Natal only a single (sexually dimorphic) species of model occurs; correspondingly *Pseudacraea* has only one sexually dimorphic form. A few species of *Bematistes* seem to occur for which *Pseudacraea* has so far not yet evolved mimetic forms. Contrary to the title of this paper, these various mimetic forms do not form various degrees of speciation. In fact, mimetic polymorphism is one of the most interesting proofs against sympatric speciation.

Structure of a butterfly population.[15]—Fisher, Ford, and Dowdeswell continue their exceedingly useful population studies. Live butterflies are marked with cellulose paint in such a manner as to indicate area and date of capture, and then again released. The work was done on the uninhabited island of Tean in the Scilly Islands. Three areas with long grass were found to be suitable for the investigated species of butterfly, but were separated from each other by unsuitable areas that proved to be powerful distributional barriers. Fixed numbers of butterflies were caught each day in each area, and the size of each population as well as the daily rate of elimination (by death or emigration) calculated. This was about 11 per cent, though higher (up to 25 per cent?) in the exposed area 5. The largest numbers flying in one day were about 1,400 individuals in area 1, about 7,000 in area 2, and 100–250 in area 5. A few recaptures (about 2 per cent) proved shifts from one area to another. This indicates a sizeable amount of gene flow between the colonies and accounts for the absence of visible differences between them. The smallest colony appeared not to be self-sustaining.

This and similar studies on bird and mammal populations have shed a great deal of light on the structure of populations and the interchange of individuals between neighboring populations. Since the evolutionary effect of immigration is measured by the share of genic change contributed by new arrivals in a population, one would like to know something about their genetic constitution. This unfortunately is not known in most of the population studies so far conducted. It seems to me that it will be exceedingly difficult to fill this gap in our knowledge. This by no means deprives population studies of their value. In fact, the numerous other gaps in our knowledge of populations make an increase in the number of such studies highly desirable. The present study is particularly recommended for the efficiency of its planning and its evaluation, two qualities which are of course expected in any work in which R. A. Fisher participates.

Genic constitution and evolutionary trends.[16]—In this review paper Kosswig discusses the difficult question to what extent parallelisms in evolution are due to homologous genes. First, the genetic evidence for homologous genes is discussed, color genes in rodents and other mammals, eye color loci in *Drosophila* and other insects (*Ephestia, Habrobracon*), and finally the pigment genes in cyprinodonts. Numerous homologies among gene loci of close relatives are well established, but it seems to me that the author is rather too liberal in calling genetic similarities homologies when the involved species belonging to orders (rodents-carnivores-lagomorphs) that have been separated at least since the Paleocene. The chromosomes have been modified so drastically since that time that the concept of homology must have become something rather nebulous. It is well known that many physiological processes and biochemical reactions have a venerable evolutionary history in the organic world. But there is no need to believe that their genetic basis has always stayed the same, especially in view of pleiotropic genes and polygenic characters. The frequency of pericentric inversions discovered in recent *Drosophila* work also warns to caution.

In the second section Kosswig describes a number of cases of parallel evolution among fishes, such as the development of very similar gonopodia in the males of four (or five) vivip-

[15] Dowdeswell, W. H., R. A. Fisher, and E. B. Ford. 1949. The quantitative study of populations in the Lepidoptera. 2. *Maniola jurtina* L. Heredity, **3**: 67–84

[16] C. Kosswig. 1948. Homologe und analoge Gene, parallele Evolution und Konvergenz. Communications Fac. Sci. Univ. Ankara, **1**: 126–177.

arous families of the order of cyprinodonts, vivipary in general, the mouth-breeding habits in cichlids, etc. Kosswig comes to the conclusion that there are usually sufficient differences among these independently evolved structures to assume analogous rather than homologous genes. However, there is often a common genetic background which preadapts for a given evolutionary trend, as has so often been described by paleontologists and has been shown for recent genera by Mayr and Vaurie (1948) and by Michener (1949) in this journal.

Genetics of the recombination spindle.[17]—E. Anderson has pointed out repeatedly that in species hybrids only a fraction of the possible recombinations of the parental characters is found. For a set of three characters the actual F_2 individuals are distributed on a three-dimensional grid in the form of a spindle ("recombination spindle") which points towards the means of the parental characters. Dempster in a most ingenious mathematical analysis shows that the amount of the restriction of recombination (the "slenderness" of the multidimensional spindle) is the higher the greater the number of loci affecting the total genetic difference between the parents. Linkage has the effect of increasing the variation of F_2 character combination in the direction of the parental types ("length of the spindle"), the more so the greater the number of loci is in comparison with the number of chromosomes. I wonder whether the shape of the recombination spindle could not be used to estimate the number of loci contributing to the difference between two species? (see op. cit., table 1).

One plant geneticist's concept of species.[18]—Species are phenomena of nature and should be studied in nature. They can be understood only if all aspects of species are considered simultaneously. The failure to understand this was in part responsible for the alienation between taxonomists and geneticists that typified the first three decades of this century. We thought that this narrowness was a matter of the past but this does not seem to be the case. In the present paper Lamprecht attempts "to clarify the species concept as exclusively as possible on the basis of the exact science of genetics." "Species," in this connection, are by implication the sample used by the plant breeder. The author presents his data as if he were completely unaware of the entire non-botanical speciation literature and defines species strictly on a sterility basis. The conclusions of the author are based on a genetic analysis of two species of cultivated beans, *Phaseolus vulgaris* and *coccineus*. Whenever two or more species can be artificially crossed and form more or less fertile F_1 and F_2 they are pronounced subspecies by the author. This reduction of taxonomic rank is no doubt frequently justified, since older authors have been very liberal in awarding species rank to recognizable populations, but should not the decision be deferred until the respective entities are examined in nature? Why should two overlapping forms be called subspecies if their flowering seasons are so far apart that no interbreeding occurs in nature? One has to think only of the two species of birds, mallard and pintail, to appreciate the absurdity of the author's species concept when applied to animals. His discovery of incompatible alleles in related good species is interesting but should not have been made the basis of such sweeping conclusions. A number of new terms is introduced by the author, including "superspecies" for polyploids, apparently in ignorance of the earlier (since 1931) use of this term in zoology for a very different type of phenomenon.

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[17] E. R. Dempster. 1949. Effects of linkage on parental-combination and recombination frequencies in F_2. Genetics, **34**: 272–284.

[18] H. L. Lamprecht. 1949. Systematik auf genischer und zytologischer Grundlage. Agri. Hortique Genetica, **7**: 1–28.

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arous families of the order of cyprinodonts, viviparity in general, the mouth-breeding habits in cichlids, etc. Kosswig comes to the conclusion that there are usually sufficient differences among these independently evolved structures to assume analogous rather than homologous genes. However, there is often a common genetic background which preadapts for a given evolutionary trend, as has so often been described by paleontologists and has been shown for recent genera by Mayr and Vaurie (1948) and by Michener (1949) in this journal.

Genetics of the recombination spindle.[5]—E. Anderson has pointed out repeatedly that in species hybrids only a fraction of the possible recombinations of the parental characters is found. For a set of three characters the actual F_2 individuals are distributed on a three-dimensional grid in the form of a spindle ("recombination spindle") which points towards the means of the parental characters. Dempster in a most ingenious mathematical analysis shows that the amount of the restriction of recombination (the "slenderness" of the multidimensional spindle) is the higher the greater the number of loci affecting the total genetic difference between the parents. Linkage has the effect of increasing the variation of F_2 character combination in the direction of the parental types ("length of the spindle"), the more so the greater the number of loci is in comparison with the number of chromosomes. I wonder whether the shape of the recombination spindle could not be used to estimate the number of loci contributing to the difference between two species? (See op. cit., table 1).

One plant geneticist's concept of species.[6]—Species are phenomena of nature and should be studied in nature. They can be understood only if all aspects of species are considered simultaneously. The failure to understand this was in part responsible for the alienation between taxonomists and geneticists that typified the first three decades of this century. We thought that this narrowness was a matter of the past but this does not seem to be the case. In the present paper Lamprecht attempts "to clarify the species concept as exclusively as possible on the basis of the exact science of genetics." "Species," in this connection, are by implication the sample used by the plant breeder. The author presents his data as if he were completely unaware of the entire non-botanical speciation literature and defines species strictly on a sterility basis. The conclusions of the author are based on a genetic analysis of two species of cultivated beans, *Phaseolus vulgaris* and *coccineus*. Whenever two or more species can be artificially crossed and form more or less fertile F_1 and F_2 they are pronounced subspecies by the author. This reduction of taxonomic rank is no doubt frequently justified, since older authors have been very liberal in awarding species rank to recognizable populations, but should not the decision be deferred until the respective entities are examined in nature? Why should two overlapping forms be called subspecies if their flowering seasons are so far apart that no interbreeding occurs in nature? One has to think only of the two species of birds, mallard and pintail, to appreciate the absurdity of the author's species concept when applied to animals. His discovery of incompatible alleles in related good species is interesting but should not have been made the basis of such sweeping conclusions. A number of new terms is introduced by the author, including "superspecies" for polyploids, apparently in ignorance of the earlier (since 1931) use of this term in zoology for a very different type of phenomenon.

---

[5] E. R. Dempster. 1949. Effects of linkage on parental-combination and recombination frequencies in F_2. Genetics, 34: 272–284.

[6] H. L. Lamprecht. 1949. Systematik auf genetischer und zytologischer Grundlage. Agri Hortique Genetica, 7: 1–28.

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Prepared by the National Research Council Committee on Common Problems in Genetics, Paleontology, and Systematics, this book by leaders in both genetics and paleontology shows how each field can use the other's contribution to the problem of evolution.

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T. Just
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